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Is larval dispersal a necessity for decapod crabs from the Amazon mangroves? Response of *Uca rapax* zoeae to different salinities and comparison with sympatric species

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ABSTRACT

Salinity may play an important role in the larval Biology and Ecology of many brachyuran decapod crustaceans. Usually, ontogenetic changes in salinity tolerance represent a good indicator of larval dispersal in marine coastal ecosystems. In an experimental laboratory study, we investigated the effects of eight different salinities (Sal. 0–35) on zoeal development of the neotropical fiddler crab *Uca rapax* from a northern Brazilian estuary. In the study area the species reproduces year-round, including the wet season when low salinities (≤5) are frequent, resulting from heavy tropical rainfalls and input of freshwater mostly from the Amazon River. Larval survival and development duration from hatching to megalopa of *U. rapax* were significantly affected by salinity. All larvae died in Sal. 0–20, while they successfully developed through five zoeal stages to megalopa in higher salinities (Sal. 25–35). However, in Sal. 25 the survival rate was still significantly lower (33.8 ± 4.8%) and the zoeal development duration was longer (13.7 ± 0.5 days) than in salinities 30 and 35, where >90% of the larvae successfully survived after an average of 11.8–12.4 days of development, respectively. Our results strongly suggest that the early life-history stages of *U. rapax* perform ontogenetic migrations towards adjacent coastal or fully marine waters to develop in favourable high salinities. Comparison with two other sympatric crab species, e.g. *Ucides cordatus* and *Uca vocator*, suggests that the larval 'export' strategy is a convergent adaptation exhibited by decapod species in the Amazon region to avoid mass mortality within parental mangroves that are frequently subjected to strong salinity fluctuations caused by the specific meteorological and hydrological conditions.

1. Introduction

Many brachyuran decapod crustaceans develop through a complex life cycle involving a meroplanktonic larval and a sedentary benthic juvenile/adult phase. Their larval development time ranges from a few days to several weeks or months in the planktonic environment before metamorphosing and changing to a benthic lifestyle (Anger, 2001, 2006). However, during the time spent in the plankton, the larvae may experience strong temporal and spatial changes in temperature, salinity, food availability and predation pressure (Anger, 2001, 2006; Morgan, 1990, 1995). Among these environmental factors, salinity may play a key role in the Biology and Ecology of decapod crustacean larvae (for review see Anger, 2001, 2003). Consequently, ecological and physiological adaptations to highly variable conditions of salinity are particularly important in species inhabiting physically extreme habitats such as mangroves and estuaries (reviewed by Anger, 2003; Charmantier, 1998).

In general, although early and advanced benthic life-history stages of decapod crustaceans are well adapted, e.g. exhibiting hyper-/hypo-osmoregulatory functions to tolerate salinity conditions ranging from hypersaline to oligohaline or freshwater levels, their meroplanktonic larval stages are physiologically more sensitive to cope with strong salinity variations that typically occur in the habitat of the conspecific benthic population (Anger and Charmantier, 2000; Charmantier, 1998; Charmantier et al., 1998, 2002). As a result, many decapod species

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developed a specific type of reproductive strategy consisting of ontogenetic migrations (i.e. larval 'export', Strathmann, 1982) of the newly hatched larvae towards coastal or fully marine waters for successful development in more stable and, on average, higher salinity conditions (Anger, 2001, 2003; Anger et al., 1994, 2000, 2008a). The downstream migration is facilitated by physical mechanisms of larval transport (e.g. outflowing tides, wind- and buoyancy-induced currents), endogenous rhythms in synchrony with ebb tides (i.e. vertical migrations) and spawning migrations of ovigerous females towards the lower parts of the estuaries or open sea (Epifanio and Garvine, 2001; Forward et al., 2003; López-Duarte et al., 2011; Queiroga and Blanton, 2005). This life-history strategy seems to be strongly correlated with ontogenetic changes in salinity tolerance and osmoregulatory capability of decapod larvae (Anger and Charmantier, 2000; Anger et al., 1990, 2008a,b; Charmantier, 1998; Charmantier et al., 2002). Larval export has been observed in several estuarine and freshwater-inhabiting crab species (e.g. *Uca pugnax*: O'Connor and Epifanio, 1985; *Sesarma angustipes*: Anger et al., 1990; *Eriocheir sinensis*: Anger, 1991; *Neohelice granulata*: Anger et al., 1994, 2008a; Charmantier et al., 2002; *Armases miersii*: Anger, 1996; Schuh and Diesel, 1995a; *Sesarma curacaoense*: Schuh and Diesel, 1995b; *Armases roberti*: Diesel and Schuh, 1998; *Armases rubripes*: Luppi et al., 2003; *Ucides cordatus*: Diele and Simith, 2006; *Uca vocator*: Simith et al., 2012). After completing the zoeal development in offshore waters, the larvae, already in the megalopal stage, migrate back upstream to the mangroves or limnic environments where the conspecific populations are found (Forward and Tankersley, 2001; Queiroga, 1998, 2003; Tankersley and Forward, 1994; Torres et al., 2006).

In the present study, we investigate the effects of salinity on zoeal development of the neotropical mangrove fiddler crab *Uca rapax* (Smith, 1870) from the Amazon region (North Brazil). Studies addressing the effects of salinity on the ontogenesis of fiddler crab species are relatively scarce (e.g. *U. pugnax*: O'Connor and Epifanio, 1985; *Uca minax*: Epifanio et al., 1988; *Uca subcylindrica*: Rabalais and Cameron, 1985; *Uca tangeri*: Spivak and Cuesta, 2009; *U. vocator*: Simith et al., 2012). *U. rapax* is a semi-terrestrial crab species distributed along the Atlantic coast of the subtropical and tropical Americas (Melo, 1996). In North Brazil, this crab species inhabits the high- to mid-intertidal zones of the mangrove forest habitat (Diele et al., 2010; Koch and Wolff, 2002; Koch et al., 2005). Their larval development comprises 5 zoeal stages followed by the megalopa (Pires, 2008). In the mangroves of the Caeté River estuary, North Brazil (Fig. 1), *U. rapax* reproduces year-round, including the wet season (January to June) (Koch et al., 2005) when extremely reduced salinities (≤5) are frequently found in estuarine waters (Diele and Simith, 2006) as a consequence of elevated precipitation rates that ranges from 1085 to 3647 mm (averages between 2500 and 3000 mm/year^{-1}; Inmet, 2008; MADAM, unpublished data). In addition, freshwater discharges from local rivers (e.g. the Amazon) have a significant influence on the salinity variations along the North Atlantic coast (see Dessier and Donguy, 1994; Geyer et al., 1996; Hu et al., 2004; Masson and Delecluse, 2001; Muller-Karger et al., 1995). Consequently, early life-history stages of *U. rapax* may experience strong hypo-osmotic stress and ontogenetic migrations towards offshore waters for development in higher salinities could thus be an important ecological adaptation to avoid larval mortality within the parental mangrove habitat. Here, we hypothesize that low salinities negatively affect survival and development of *U. rapax* larvae.

In the present laboratory study we experimentally investigate the effects of eight different levels of salinity on (i) larval survival and development duration from hatching to megalopa, and on (ii) survival and duration of each zoeal stage of the mangrove fiddler crab *U. rapax*. The ontogenetic pattern of survival in response to different test salinities serves as an indicator of larval dispersal (or larval 'retention', Strathmann, 1982) in the study area. This was already shown for sympatric crab species such as *U. cordatus* (Diele, 2000; Diele and Simith, 2006; Simith and Diele, 2008) and *U. vocator* (Simith et al., 2012), which share the same microhabitat as *U. rapax* (Diele et al., 2010; Koch and Wolff, 2002; Koch et al., 2005). The ontogenetic changes in larval salinity tolerance of *U. rapax* are discussed and compared with these two other co-occurring crab species from the northern Brazilian mangroves.

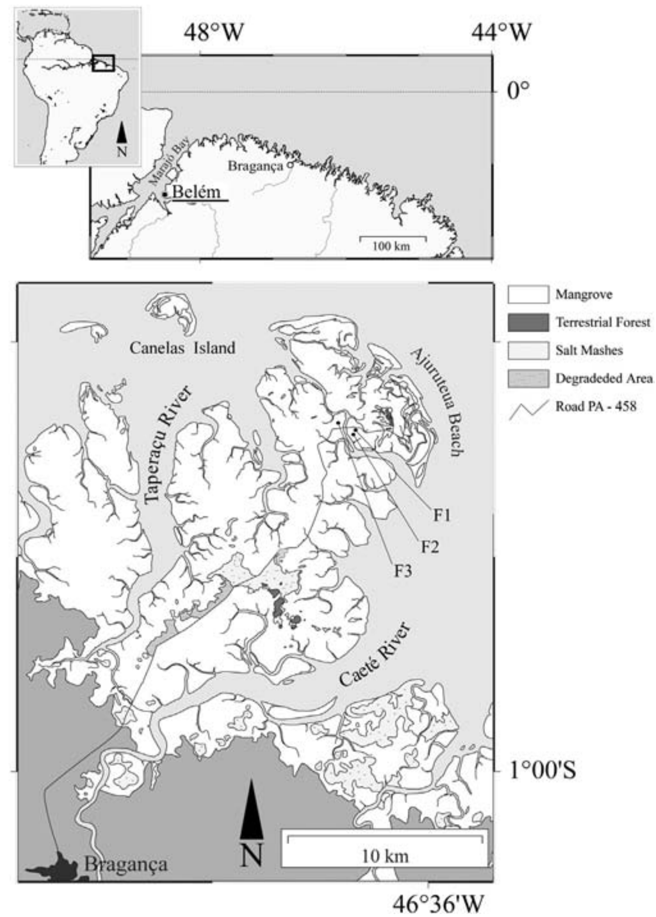

Fig. 1. Caeté River estuary located in the Amazon region, North Brazil. F1–F3 = sites of collection of the three ovigerous females of the fiddler crab *Uca rapax*.

2. Materials and methods

2.1. Cultivation medium

Seawater for larval cultivation (salinity 35) was obtained 50 km offshore the northern Brazilian coast. In the laboratory, the water was firstly filtered (Eheim and Diatom Filter, 1 μm), sterilised (ultraviolet filter: Gehaka) and stored in tanks (500 L) with constant aeration. Sodium hypochlorite (2.5%) was added weekly (0.5 mL per litre seawater) for additional sterilisation. The filtered seawater was diluted with appropriate amounts of distilled tap water for obtaining the different test salinities for zoeal cultivation (see below). Salinity was measured with a WTW-LF 197 probe and with a hand refractometer (S/Mill-E, Atago). As the distilled tap water (Sal. 0) and the diluted seawater (Sal. 5, 10 and 15) were slightly acidic (pH ≤ 5.1), we adjusted pH values to 7.5–8.1 using biological filters built with sterile calcareous substratum (e.g. shells). This calcareous medium provides sodium carbonate and sodium bicarbonate ions (buffering substances), which are slowly dissolved into the water, thus increasing and stabilising pH. A pH-metre probe (pH-710, Instrutherm) was used to measure the pH values of the cultivation water.