Influence of natural settlement cues on the metamorphosis of fiddler crab megalopae, *Uca vocator* (Decapoda: Ocypodidae)

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ABSTRACT

Megalopae of many decapod crab species accelerate their development time to metamorphosis (TTM) when exposed to natural physical and/or chemical cues characteristic of the parental habitat. In the present study, the influence of natural settlement cues on the moulting rates and development TTM in megalopae of the fiddler crab *Uca vocator* was investigated. The effects of mud from different habitats (including well-preserved and degraded-polluted mangrove habitats) and conspecific adult 'odours' (seawater conditioned with crabs) on the induction of metamorphosis were compared with filtered pure seawater (control). 95 to 100% of the megalopae successfully metamorphosed to first juvenile crab stage in all treatments, including the control. However, the development TTM differed significantly among treatments. Settlement cues significantly shortened development, while moulting was delayed in their absence. The fact that megalopae responded to metamorphosis-stimulating cues originating from both adult and non-adult benthic habitats demonstrates that settlement in this species may occur in a wider range of habitats within the mangrove ecosystem, including impacted areas.

Key words: conspecific 'odours', fiddler crab, megalopa, metamorphosis, settlement, Uca vocator.

INTRODUCTION

The transition from the planktonic to benthic environment is considered as a critical phase within the complex life cycle of many marine and estuarine invertebrates that are sedentary or sessile as adults. Settlement and metamorphosis are important biological processes in this critical transition (Anger 2001, 2006, Forward et al. 2001, Gebauer et al. 2003). For the last planktotrophic settlement larval stage (megalopa) of several decapod crab species, these processes are triggered by specific natural physical and/or chemical stimuli, which are commonly associated to the habitat where conspecific juveniles and adults live (for review see Anger 2001, 2006, Forward et al. 2001, Gebauer et al. 2003).

The type of substratum, characteristic for the par-

ental habitat (or substratum-associated cues, e.g. microbial biofilms) and water soluble chemical 'odours' (pheromones?) released by conspecific adult crabs have been demonstrated as effective in accelerating the development time to metamorphosis (TTM) in megalopae of many decapod crab species as, for instance, in *Panopeus herbstii* (Weber and Epifanio 1996, Rodriguez and Epifanio 2000, Andrews et al. 2001), *Rhithropanopeus harrisii* (Fitzgerald et al. 1998), *Chasmagnathus granulata* (Gebauer et al. 1998), *Sesarma curacaoense* (Gebauer et al. 2002), *Hemigrapsus sanguineus* (Kopin et al. 2001, O'Connor 2008, Steinberg et al. 2007, 2008), *Dyspanopeus sayi* (Kopin et al. 2001), *Armases roberti* (Anger et al. 2006), *Ucides cordatus* (Diele and Simith 2007, Simith and Diele 2008) and *Menippe mercenaria* (Krimsky and Epifanio 2008). In the absence of suitable natural settlement cues, the development TTM can

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be delayed for several days to months, which may result in significant costs to the post-metamorphic benthic crab stages (Anger 2001, Gebauer et al. 1999, 2003). In addition, the metamorphic moult also seems to be inducible by natural benthic microbial biofilms, as suggested by several authors (e.g. Weber and Epifanio 1996, O'Connor and Judge 1997, Rodriguez and Epifanio 2000, O'Connor and Van 2006, O'Connor 2008, Steinberg et al. 2008, Krimsky and Epifanio 2008). It is assumed that biofilms absorb, store and, thereby, increase the concentration of water-soluble chemical molecules (Decho 1990), such as those emitted by adult crabs (e.g. chemical 'odours' or pheromones) (O'Connor and Van 2006).

In fiddler crab species (Ocypodidae), to our knowledge, the effect of environmental cues on metamorphosis has so far only been studied in *Uca pugilator* (Christy 1989, O'Connor 1991), *U. pugnax* (O'Connor and Judge 1997, 1999, O'Connor and Gregg 1998, O'Connor 2005, O'Connor and Van 2006) and *U. minax* (O'Connor and Judge 2004). Laboratory and field experiments demonstrated that the development TTM is shortened in the presence of environmental cues in these species. The acceleration of metamorphic moult was primarily observed when megalopae were reared on mud substratum from the adult habitat collected near conspecific crab burrows (Christy 1989, O'Connor 1991, O'Connor and Judge 1997, 1999, O'Connor and Van 2006) and when specimens were exposed to waterborne cues in seawater overlying marshes (O'Connor and Judge 1997, 1999, 2004). However, the effectiveness of environmental cues in salt marshes seems to decrease with increasing distance from the adult habitat (O'Connor and Judge 2004). Water-soluble chemical 'odours' and chemical extracts (e.g. proteins solutions) from adult crabs have also been found as effective metamorphosis-stimulating cues for megalopae in these fiddler crab species (O'Connor 1991, 2005, O'Connor and Gregg 1998, O'Connor and Van 2006). Furthermore, the combination of substratum and conspecific adult 'odours' caused a stronger accelerating effect on the development TTM than the influence of individual cues (O'Connor 1991, O'Connor and Van 2006).

In the present paper, we investigate the influence of environmental cues on the settlement of megalopae of the fiddler crab *U. vocator* (Herbst 1804). In our ex-

periment, the effects of mud taken from different mangrove habitats (including well-preserved and degraded-polluted habitats) and conspecific adult 'odours' (seawater conditioned with crabs) were investigated by means of moulting rates and development duration of the megalopal stage. *U. vocator* is a semi-terrestrial fiddler crab that digs burrows in high-intertidal sediments in mangroves and estuaries (Melo 1996, Koch and Wolff 2002, Koch et al. 2005, J.F. Lima, unpublished data). This species occurs along the coast of the Americas (Gulf of Mexico, Central America, Antilles, North of South America, Guyana and, in Brazil, from Pará to Santa Catarina State) (Melo 1996, J.F. Lima, unpublished data). In Northern Brazil, *U. vocator* reproduces during the rainy season (Koch et al. 2005). Its larval development comprises four to six zoeal stages and a megalopa (Rieger 1999).

It is still unknown where the larvae of this species develop. For several other fiddler crabs, it was shown that ebb tides disperse their larvae to coastal waters (see Dittel and Epifanio 1982, Lambert and Epifanio 1982, Epifanio 1988, Epifanio et al. 1988, Dittel et al. 1991). After reaching the megalopal stage, the larvae return to the parental habitat type (Brookins and Epifanio 1985, Epifanio et al. 1988, Little and Epifanio 1991, De Vries et al. 1994) and settle near conspecific adults (O'Connor 1993), guided by environmental cues typical for the adult habitat. The larvae of *U. vocator* in our N-Brazilian study area are also likely to be exported to coastal or marine waters due to the prevailing strong macrotidal regime and high larval mortality in low salinity waters (D.J.B. Simith et al., unpublished data). Furthermore, *U. vocator* spawns at spring ebb tides, thereby promoting offshore dispersal, as was shown for the co-occurring mangrove crab *U. cordatus* (Diele and Simith 2006). Hence, we hypothesize that ready-to-settle *U. vocator* megalopae respond positively to natural physical and/or chemical cues attracting them back to the semi-terrestrial mangrove habitat.

MATERIALS AND METHODS

SEAWATER FOR CULTIVATION

Seawater (salinity 35) was collected 35 km off the Bragantine peninsula (Northern Brazil) well behind the estuarine plume to avoid chemical cues from mangroves.

The water was filtered (Eheim and Diatom Filter: 1μm) and stored in tanks (500 l) with constant aeration. Sodium hypochlorite (2.5%) was added weekly (1 ml per liter seawater) for sterilization. Deionised tap water was used for dilution in order to obtain salinity 20 for cultivation, which is one of the optimum salinities for high larval survival in this species (D.J.B. Simith et al., unpublished data).

LARVAL ORIGIN AND REARING CONDITIONS

Larvae of *U. vocator* were obtained from 5 ovigerous females captured one day before hatching in the mangroves of the Caeté River estuary (northeastern region of the State of Pará, Northern Brazil). In the Laboratory of Carcinology at the Campus of the Federal University of Pará (Bragança city), the females were washed, gradually acclimatized (increasing five units of salinity at each hour) and kept individually in 5 liters of filtered seawater (constant 26°C, salinity 20 and pH 8.0) in separated glass aquaria until larval release. After spawning, the freshly hatched zoea larvae of the five females were mixed in a glass beaker (500 ml). Groups of 20 larvae were transferred to plastic vials (250 ml) using widebore pipettes. The larvae were reared without aeration, at $28.1 \pm 1.2°$C, pH 8.0 ± 0.1, salinity 20 and 12 h: 12 h/ light: dark photoperiod cycle. The zoea larvae were fed daily with microalgae *Dunaliella salina* and *Thalassiosira* sp., rotifers *Brachionus plicatilis* (at a density of approximately 20 rotifers-ml^{-1}) and newly-hatched brine-shrimp *Artemia* sp. nauplii (approximately 5 nauplii-ml^{-1}). The latter were only added in the cultivation when larvae had reached the third zoeal stage. The cultivation water was changed at every three days. Larvae were checked daily for mortality and moults. The rearing conditions of the megalopal stage were the same as for the zoea larvae; however this stage was fed with *Artemia* sp. (approximately 2 nauplii-ml^{-1}) only.

EXPERIMENTAL DESIGN

For evaluating a possible metamorphosis-stimulating effect of mud and conspecific adult 'odours' on moulting rates and the development TTM of *U. vocator*, 420 freshly-moulted megalopae were randomly distributed among seven treatments, including a control group (see Table I). Each treatment was carried out with three replicates vials containing 20 megalopae each. Cannibalism did not occur during cultivation. The larvae developed through five zoeal stages and were between 10 to 16 days old when they moulted to megalopal stage. Different aged specimens were equally distributed among treatments.

At every seawater change (3 to 4 days), newly collected substrata (10 g were added to the bottom of the cultivation vials) and fresh conspecific adult 'odour' cues (for experimental set-up and treatments see Table I) were provided. Megalopae were monitored daily for mortality and moult to first juvenile crab stage. The experiment was conducted until the last megalopae had reached metamorphosis or died in the respective experimental and control treatments.

STATISTICAL ANALYSIS

The effects of the different treatments were analyzed comparing moulting rates (= percentage of metamorphosis) and average development TTM of the megalopal stage. The day of moulting to megalopa was defined as day 0 for the determination of the megalopal age and development TTM in the respective experimental and control treatments.

All statistical analysis followed standard techniques Sokal and Rohlf 1995). The moulting rates were analyzed by contingency tables (rows $\times$ columns) followed by Chi-squared tests. For the development TTM, normality and homogeneity of variance were checked *a priori* by means of the Kolmogorov-Smirnov's and Levene's median tests, respectively. Data did not show the prerequisites for parametric statistics; therefore, the Kruskal-Wallis's *H*-test was applied. Multiple *a posteriori* comparisons (Dunn's test or Mann-Whitney's *U*-test) were performed to identify pair-wise differences among experimental treatments. Differences were considered significant when $P < 0.05$.

RESULTS

Moulting rates of *U. vocator* megalopae did not differ among the seven treatments, including the control group ($P > 0.05$). The percentage of megalopae that had undergone metamorphosis to the first juvenile crab stage was always high (95 to 100%) (Fig. 1).

In contrast to moulting rates, the average values of

TABLE I
Experimental design for cultivation of *Uca vocator* megalopae.

Treatments	Description
1 – ACW: *Adult-conditioned seawater*	10 adult males and 10 females of *U. vocator* (carapace width = 2.03 ± 025 and 1.35 ± 0.15 cm, respectively) were immersed for 24 h in 2 liters of filtered seawater with constant aeration. Thereafter, the crabs were removed; the water was sieved (100μm) and immediately used for cultivation.
2 – M1: *Mud from preserved mangrove (PM) inhabited by conspecific adults*	Mud was collected from the upper three centimetres of sediment surface near the openings of conspecific adult burrows in PM.
3 – ACW + M1	ACW combined with M1 from PM.
4 – M2: *Mud from channel bank within PM, not inhabited by conspecific adults*	Mud was collected from the upper three centimetres from a mid-intertidal channel bank within PM. The locality is populated by *U. maracoani* only.
5 – M2 + S: *Muddy sand from PM void of conspecifics*	A natural mixture of mud and sand was collected ten centimetres below ground from a mid-intertidal mud bank within PM. Hereafter referred to as muddy-sand.
6 – M3: *Mud from degraded mangrove (DM) inhabited by conspecific adults*	Mud was obtained near *U. vocator* burrows in DM (see below site description).
7 – *Control treatment* (C)	Filtered pure seawater.

DM (degraded mangrove habitat) is located in Bragança city (northeastern region of the State of Pará, Northern Brazil) on the banks of the Caeté River. Part of the mangrove was deforested for human occupation. The locality is eutrophized and polluted by sewage and trash. *U. vocator* is the dominant species with a density of up to 6 specimens/m^2 (D.J.B. Simith, personal observations).

development time to metamorphosis (TTM) were significantly shorter ($P < 0.05$) in treatments with environmental cues than in the seawater control, where the development was slowest, taking 13.6 ± 1.5 days (Fig. 2). The second longest average development TTM occurred in the treatment with mud from a degraded-polluted mangrove habitat populated by conspecific adults (M3) (Fig. 2). On mud from a well-preserved adult-populated mangrove habitat (M1) and on muddy-sand from the mid-intertidal mud bank void of conspecifics (M2 + S), whose TTM were similar, the development was significantly faster ($P < 0.05$) than in all other treatments (Fig. 2). Average development TTM of the megalopae reared in the treatments with conspecific adult 'odours' (ACW) and on substratum from a mid-intertidal mud bank (M2) did not differ ($P > 0.05$) from each other (Fig. 2).

The development TTM ranged from 4 to 16 days and in five out of the seven treatments juvenile crabs began to appear by day 5 (Fig. 1). In the treatments M1 and M2 + S, > 50% of metamorphosis (cumulative percentage) occurred on day 6, while no megalopa had moulted by this time in the seawater control (Fig. 1). In adult-conditioned seawater combined with mud (ACW + M1) and on mud from atypical habitat (M2), > 50% of the specimens had metamorphosed by day 7 (Fig. 1). In ACW, the 50% value was reached on day 8 and on day 9 in M3 (Fig. 1). In the seawater control, > 50% of metamorphosis occurred only on day 14 (Fig. 1).

DISCUSSION

In the present study, high percentages of megalopae metamorphosed to the first juvenile crab stage in all seven treatments, including the seawater control and, thus, irrespective of the presence and/or nature of the tested environmental cues. These included substrata from well-
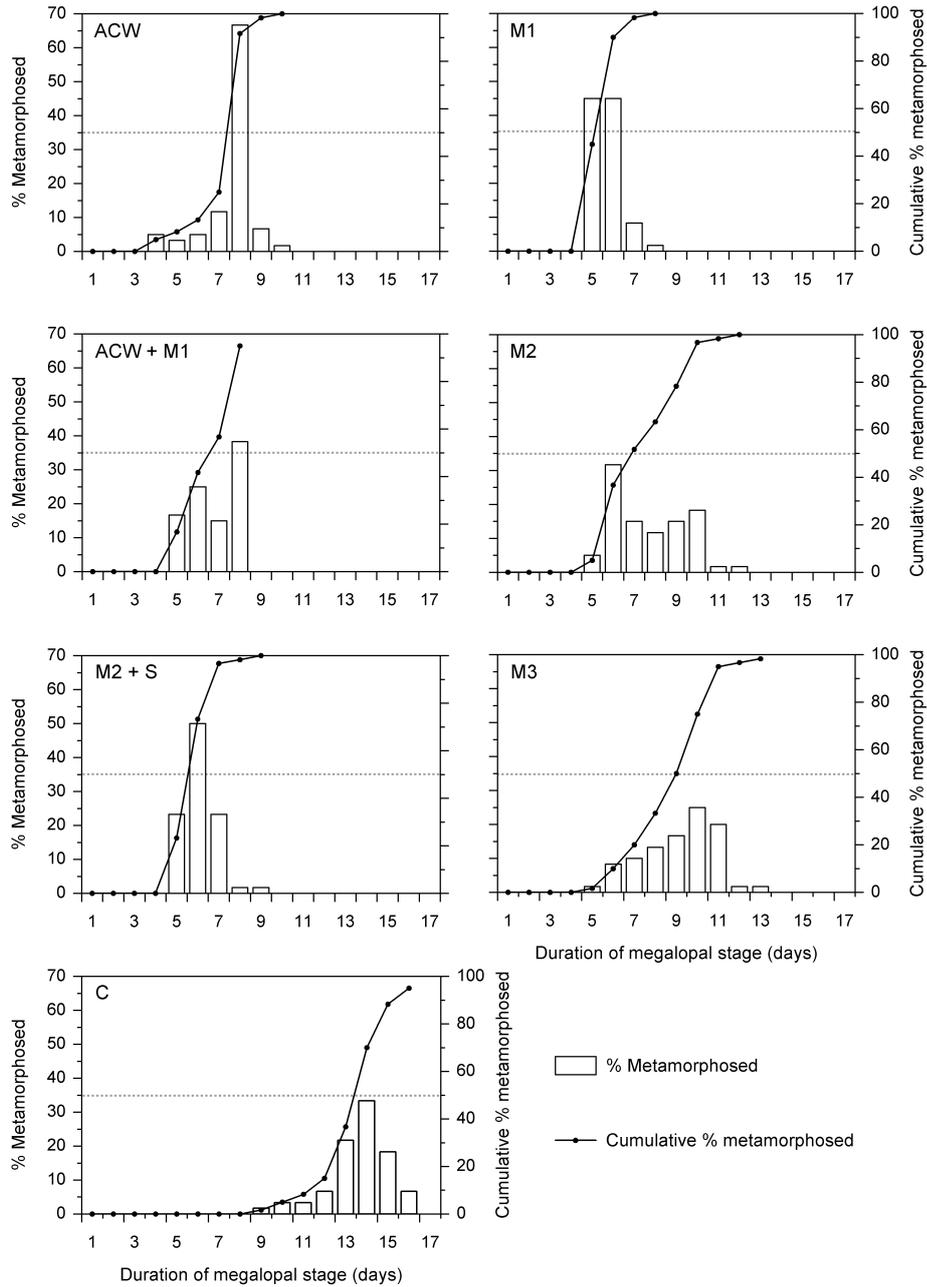
Fig. 1 – Percentage of metamorphosed *U. vocator* megalopae in the treatments with natural settlement cues from different mangrove habitats (well-preserved and degraded habitats), with adult-conditioned seawater and filtered pure seawater. Pooled data from three replicate vials. See Table I for abbreviations. Dashed lines indicate 50%.

preserved (PM) and degraded-polluted (DM) mangrove habitats, both populated by conspecific crabs; substrata from 'atypical' habitats within PM void of conspecifics, such as mud or muddy-sand from a mid-intertidal mud bank; and conspecific 'odours' released by adult crabs into seawater. Hence, regarding the rate of moulting, the metamorphic response of *U. vocator* seems to be

rather unspecific. This is in sharp contrast to other *Uca* species that showed significantly elevated moulting rates only when megalopae were exposed to environmental cues, characteristic of the parental habitat (e.g. *Uca pugilator*: Christy 1989, O'Connor 1991, *U. pugnax*: O'Connor and Judge 1997, 1999, O'Connor and Gregg 1998, O'Connor 2005, O'Connor and Van 2006, *U. mi-*
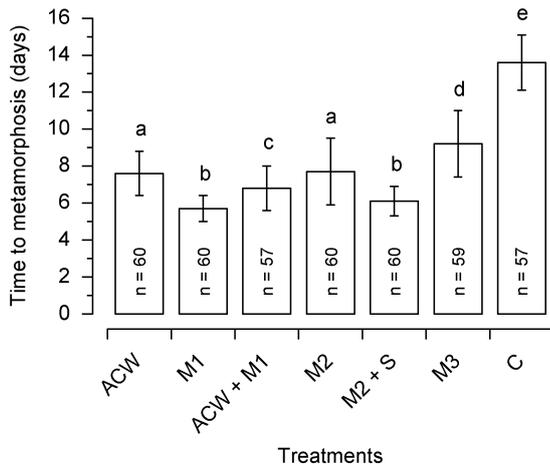
Fig. 2 – Effects of substrata from different mangrove habitats (well-preserved and degraded habitats), adult-conditioned seawater and filtered pure seawater on the development time to metamorphosis (average ± standard deviation) of *Uca vocator* megalopae. See Table I for abbreviations. Numbers inside bars refer to the number of metamorphosed megalopae with initial n = 60 specimens randomly distributed among three replicate vials per treatment. Different letters above bars indicate significant differences ($P < 0.05$) after pair-wise comparisons using Dunn's or Mann-Whitney's tests.

nax: O'Connor and Judge 2004). O'Connor and Judge (2004) found that the effectiveness of salt-marsh chemical cues in inducing the moulting response of *U. minax* megalopae significantly declined within a short distance from the adult habitat. Settlement-induction by cues typical for the adult habitat favours gregarious settlement, whereas a more habitat-unspecific metamorphic response, as observed in *U. vocator* in our study, should promote a faster establishment and spreading of new populations elsewhere along a given coastline, within the geographical range of the species. Thus, our results suggest that *U. vocator* megalopae may settle in a wide range of habitats (e.g. adult and non-adult habitats) within mangrove estuaries.

In contrast to the moulting rate, development time to metamorphosis (TTM) of *U. vocator* megalopae was significantly shorter in the treatments with physical and/or chemical environmental cues compared to the seawater control. Hence, regarding the velocity of their development, *U. vocator* megalopae do respond positively to semi-terrestrial environmental cues. The prolonged development TTM observed in seawater devoid

of appropriated cues would increase the likelihood that megalopae find a suitable habitat for settlement and transition to the benthic phase of their life-cycle. However, a delay of moulting may also result in an increased risk of predation in the plankton (Morgan 1995) and in physiological costs for the post-metamorphic juvenile crab stage (Gebauer et al. 1999). As in *U. vocator*, megalopae of *U. pugilator* (Christy 1989, O'Connor 1991) and *U. pugnax* (O'Connor and Gregg 1998, O'Connor and Van 2006) also postpone the metamorphic moult in seawater without habitat cues. Delay of metamorphosis was also recorded in many other crab species in the literature (for review see Gebauer et al. 2003).

The development TTM of *U. vocator* megalopae reared on mud from the mid-intertidal bank (M2), a habitat not populated by conspecific adults, did not differ from the specimens kept in adult-conditioned seawater (ACW). In a similar way, the development TTM of megalopae reared on mud taken near to conspecific adult burrows (M1) and on muddy-sand from the mid-intertidal bank (M2 + S) did not differ from each other. This is surprising as in other decapod crab species conspecific adult 'odours' and substrata collected within adult habitats were much more effective in accelerating metamorphosis than substrata from 'atypical' habitats or collected at various distances from the habitat where the conspecific population lives (e.g. *U. pugilator*: O'Connor 1991, *U. pugnax*: O'Connor and Gregg 1998, O'Connor and Van 2006, *U. minax*: O'Connor and Judge 2004, *C. granulate*: Gebauer et al. 1998, *U. cordatus*: Diele and Simith 2007). The effect of mud from treatment M2 on the development TTM of *U. vocator* megalopae may have resulted from 'odours' emitted by the fiddler crab *Uca maracoani*, as this species is very abundant on the mid-intertidal mud bank within the preserved mangrove habitat. The mud used in our experiment may, thus, have carried the 'odours' of these crabs and induced metamorphosis of *U. vocator* megalopae, which will be investigated in a further study. The influence of interspecific crabs on metamorphosis was already reported for several other species (e.g. *H. Sanguineus*: Kopin et al. 2001, O'Connor 2008, *P. herbstii*: Rodriguez and Epifanio 2000, Andrews et al. 2001, *S. curacaoense*: Gebauer et al. 2002, *U. cordatus*: Simith and Diele 2008). In addition, or alternatively, it is also

possible that ubiquitous biofilms (e.g. bacteria or diatom films) growing on the surface of the mud may have induced metamorphosis of *U. vocator* in the treatments M2 or M2 + S. This hypothesis will be addressed in a future study. Biofilms have been suggested to act as a source of stimulatory cues for metamorphosis in megalopae of decapod crabs for some authors in the literature (e.g. *P. herbstii*: Weber and Epifanio 1996, Rodriguez and Epifanio 2000, *U. pugnax*: O'Connor and Van 2006, *H. sanguineus*: O'Connor 2008, Steinberg et al. 2008, *Menippe mercenaria*: Krimsky and Epifanio 2008).

The development TTM of megalopae reared in treatment M1, with mud from the well-preserved mangrove, was significantly shorter than in treatment M3, with mud from the degraded-polluted mangrove habitat. As both habitats are equally populated by conspecific adults, it seems that the pollution at M3 was responsible for the delay of metamorphosis of the megalopae reared in this treatment. However, the overall rates of settlement were equal in the two treatments, suggesting that the positive effect of conspecific 'odours' released and possibly stored in the mud is more influential than a possible inhibitory effect of the pollution.

When megalopae were reared in the presence of combined cues (ACW + M1), the average development TTM was significantly shorter than in the treatment ACW only. The combination of environmental cues associated with the parental habitat, such as mud and conspecific adult 'odours', probably enhances the chances of rapidly finding a suitable site for definitive settlement close to a conspecific population. However, it remains open why treatment M1 accelerated development more than treatments ACW + M1 or ACW in our experiment. In other species, e.g. *U. pugilator* (O'Connor 1991), *C. granulata* (Gebauer et al. 1998), *U. pugnax* (O'Connor and Van 2006), *H. sanguineus* (O'Connor 2008) and *U. cordatus* (Diele and Simith 2007), substratum was more stimulatory when combined with conspecific 'odours' than by itself.

In conclusion, our experiment demonstrated that *U. vocator* megalopae metamorphose in high rates both in the presence of physical and/or chemical semiterrestrial environmental cues and in pure seawater void of such cues. However, unlike seawater, all environmental cues tested significantly accelerated the development

TTM of the megalopae, which reduces their exposure time to larval predators and may also have positive post-metamorphic effects. In addition to gregarious settlement in habitats populated by conspecific crabs, our results also suggest that *U. vocator* megalopae may settle in mangrove areas where conspecific adults are absent, possibly triggered by the presence of other crab species and/or substratum-associated cues, e.g. microbial biofilms. Such a response would clearly promote the colonization of new areas within mangroves, estuaries and still in degraded habitats not yet or not any longer populated by *U. vocator*.

RESUMO

Megalopas de muitas espécies de caranguejos decápodes aceleram seu período de desenvolvimento até a metamorfose (PDM) quando são expostas a estímulos naturais físicos e/ou químicos característicos do habitat parental. No presente estudo, a influência de estímulos naturais sobre as taxas de muda e sobre o PDM foi investigada nas megalopas do caranguejo violinista *Uca vocator*. Os efeitos da (i) lama de diferentes habitats (incluindo habitats de um manguezal bem preservado e de um degradado e poluído) e (ii) 'odores' dos adultos conspecíficos (água do mar acondicionada com caranguejos) sobre a indução da metamorfose foram comparados com (iii) água do mar pura e filtrada (controle). 95 a 100% das megalopas realizaram a metamorfose com sucesso para o primeiro estágio de caranguejo juvenil em todos os tratamentos, incluindo o controle. No entanto, o PDM diferiu significativamente entre os tratamentos. Os estímulos encurtaram significativamente o desenvolvimento, enquanto que a muda foi retardada na ausência deles. O fato de que as megalopas responderam aos estímulos indutores da metamorfose oriundos de ambos os habitats bentônicos dos adultos e de habitats onde eles são ausentes,

demonstra que o assentamento nesta espécie pode ocorrer em uma grande variedade de habitats dentro do ecossistema de manguezal, incluindo áreas impactadas.

Palavras-chave: 'odores' conspecíficos, caranguejo violinista, megalopa, metamorfose, assentamento, *Uca vocator*.

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