Anais da Academia Brasileira de Ciências
ISSN: 0001-3765
aabc@abc.org.br
Academia Brasileira de Ciências
Brasil

Anais da Academia Brasileira de Ciências (2010) 82(2): 313-321
(Annals of the Brazilian Academy of Sciences)
ISSN 0001-3765
www.scielo.br/aabc

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

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Manuscript received on February 12, 2009; accepted for publication on July 29, 2009

ABSTRACT

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

ental habitat (or substratum-associated cues, e.
crobial biofilms) and water soluble chemical '
(pheromones?) released by conspecific adult cra
been demonstrated as effective in accelerating the
opment time to metamorphosis (TTM) in megal
many decapod crab species as, for instance, in *Pa*
herbstii (Weber and Epifanio 1996, Rodriguez a
fanio 2000, Andrews et al. 2001), *Rhithropanope*
risii (Fitzgerald et al. 1998), *Chasmagnathus gr*
(Gebauer et al. 1998), *Sesarma curacaoense* (Ge
al. 2002), *Hemigrapsus sanguineus* (Kopin et a
O'Connor 2008, Steinberg et al. 2007, 2008
panopeus sayi (Kopin et al. 2001), *Armases*
(Anger et al. 2006), *Ucides cordatus* (Diele and

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 study, we examined for the first time environmental cues that may trigger metamorphosis in *Uca vocator* megalopae (Herbst 1804). In a laboratory experiment, 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

The water was filtered (Eheim and Diatom Filter: 1 μm) 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 wide-bore pipettes. The larvae were reared without aeration, at 28.1 ± 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

cates vials containing 20 megalopae each. Cann
did not occur during cultivation. The larvae dev
through five zoeal stages and were between 1
days old when they moulted to megalopal stage
ferent aged specimens were equally distributed
treatments.

At every seawater change (3 to 4 days), new
lected substrata (10 g were added to the bottom
cultivation vials) and fresh conspecific adult ‘odou
(for experimental set-up and treatments see Table
provided. Megalopae were monitored daily for
ity and moult to first juvenile crab stage. The
ment was conducted until the last megalopae had
metamorphosis or died in the respective experi
and control treatments.

Statistical Analysis

The effects of the different treatments were an
comparing moulting rates (= percentage of me
phosis) and average development TTM of the meg
stage. The day of moulting to megalopa was def
day 0 for the determination of the megalopal a
development TTM in the respective experimen
control treatments.

All statistical analysis followed standard
niques Sokal and Rohlf 1995). The moulting rate
analyzed by contingency tables (rows × colum
lowed by Chi-squared tests. For the developmen
normality and homogeneity of variance were c
a priori by means of the Kolmogorov-Smirnov
Levene’s median tests, respectively. Data did no
the prerequisites for parametric statistics; theref
Kruskal-Wallis’s H-test was applied. Multiple *a p*
ori comparisons (Dunn’s test or Mann-Whitney’s
were performed to identify pair-wise differences
experimental treatments. Differences were con
significant when $P < 0.05$.

RESULTS

Moulting rates of *U. vocator* megalopae did no
among the seven treatments, including the contro
($P > 0.05$). The percentage of megalopae that h

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)

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

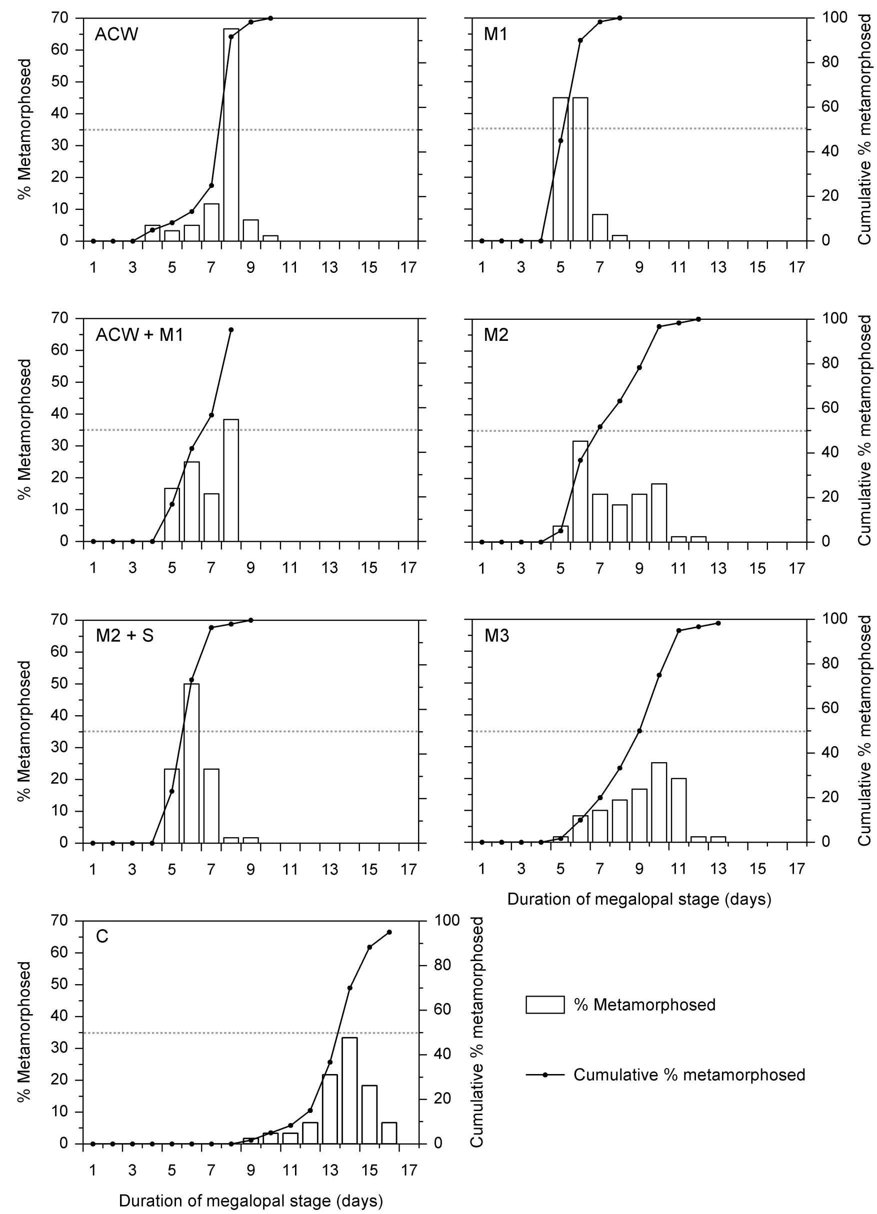

Fig. 1 – Percentage of metamorphosed *U. vocator* megalopae in the treatments with natural settlement cues from different mangrove
(well-preserved and degraded habitats), with adult-conditioned seawater and filtered pure seawater. Pooled data from three replicate v
Table I for abbreviations. Dashed lines 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

rather unspecific. This is in sharp contrast to oth
species that showed significantly elevated moultin
only when megalopae were exposed to environ
cues, characteristic of the parental habitat (e.g

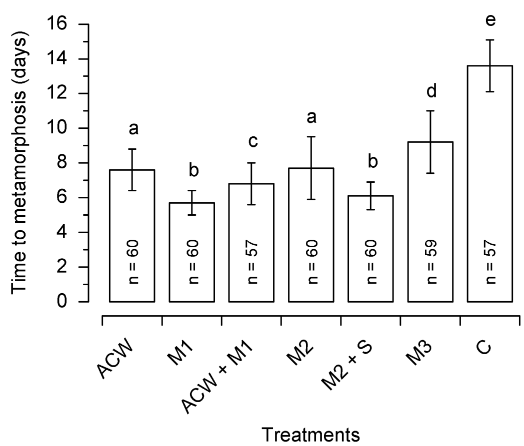

Fig. 2 – Effects of substrata from different mangrove habitats (well-preserved and degraded habitats), adult-conditioned seawater and filtered pure seawater on the development time to metamorphosis (average ± standard deviation) of *Uca vocator* megalopae. See Table I for abbreviations. Numbers inside 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 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*: Ropossible 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 semiterres-

TTM of the megalopae, which reduces their ex
time to larval predators and may also have positiv
metamorphic effects. In addition to gregarious
ment in habitats populated by conspecific crabs,
sults also suggest that *U. vocator* megalopae m
tle in mangrove areas where conspecific adults
sent, possibly triggered by the presence of oth
species and/or substratum-associated cues, e.g.
bial biofilms. Such a response would clearly p
the colonization of new areas within mangroves,
ies and still in degraded habitats not yet or not any
populated by *U. vocator*.

ACKNOWLEDGMENTS

We thank Luiz Paulo de Carvalho Melo, Adelso
de Souza and Marcus Alexandre Pires for helpin
laboratory during larval rearing and collections
and crabs. We are grateful to Dra. Cristiana R
Maciel for her support in the larval cultivation
study was financed by 'Secretaria de Desenvolvi
Ciência e Tecnologia' (SEDECT) and 'Funda
Amparo à Pesquisa do Estado do Pará' (FAPESP

RESUMO

Megalopas de muitas espécies de caranguejos decápo
leram seu período de desenvolvimento até a meta
(PDM) quando são expostas a estímulos naturais físic
químicos característicos do habitat parental. No pres
tudo, a influência de estímulos naturais sobre as taxas
e sobre o PDM foi investigada nas megalopas do car
violinista *Uca vocator*. Os efeitos da (i) lama de di
habitats (incluindo habitats de um manguezal bem pre
e de um degradado e poluído) e (ii) 'odores' dos adult
pecíficos (água do mar acondicionada com caranguejo
a indução da metamorfose foram comparados com (
do mar pura e filtrada (controle). 95 a 100% das me
realizaram a metamorfose com sucesso para o primeiro
de caranguejo juvenil em todos os tratamentos, incluind
trole. No entanto, o PDM diferiu significativamente
tratamentos. Os estímulos encurtaram significativame
senvolvimento, enquanto que a muda foi retardada na

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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