Effects of substrata and conspecific odour on the metamorphosis of mangrove crab megalopae, *Ucides cordatus* (Ocypodidae)

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Abstract

Environmental cues associated with the adult habitat induce metamorphosis in many marine invertebrate larvae and thus settlement in a place appropriate for completing their life-cycle. *Ucides cordatus* is a semi-terrestrial crab that exemplifies organisms living in mangrove estuaries as adults, but whose larvae develop offshore and return to the estuarine environment prior to metamorphosis. We investigated the influence of substrata (burrow mud, channel-bank mud, dead wood, sand, nylon mesh) and conspecific adult cues (crab conditioned seawater) on metamorphosis and the duration of the megalopal phase. Our results suggest that *U. cordatus* megalopae settle in areas populated by conspecific crabs and/or muddy habitats. High moulting rates were observed in the treatments with mud and/or adult odour (67 – 91 %), whereas in the other substrata treatments and in the seawater control less than 20% and 5% of the megalopae metamorphosed, respectively. Megalopae are also capable of delaying metamorphosis. Over channel bank mud they moulted 8 days later at an average, compared to the treatment with crab conditioned seawater. Such a delay could result in a reduced juvenile fitness. In seawater control almost all megalopae

died prior to metamorphosis, without moulting spontaneously as observed in other species. This reflects the crucial importance of habitat cues for the settlement and recruitment of this ecologically and economically important species. We outline the necessity of future research concerning post-metamorphic carry-over effects, the possible role of biofilms in absorbing and/or producing settlement cues, as well as the question whether the megalopae react specifically to the odour of *U. cordatus*, or also to other species. The latter is of particular interest against the background of the spreading lethargic crab disease that results in massive mortalities of *U. cordatus*, but not of co-occurring-species.

Key words *Ucides cordatus*; mangrove crab; megalopa; metamorphosis; settlement; habitat cue; substrata; conspecific odour

1. Introduction

Ucides cordatus cordatus (Linnaeus, 1763) (hereafter referred to as *U. cordatus*) is a large semi-terrestrial mangrove crab of the tropical and subtropical Atlantic coast of the Americas (Türkay, 1970). The crabs strongly affect litter turnover and nutrient cycling in the mangrove ecosystem (Schories et al., 2003; Nordhaus et al., 2006). In Brazil, the species is artisanally exploited (Nordi, 1994; Botelho et al., 2000; Nóbrega and Nishida, 2003; Glaser and Diele, 2004; Alves et al., 2005; Diele et al., 2005) and annual fisheries yields may reach > 7 t per km² mangrove forest (after Araújo, unpublished). Since 1997 mass mortality events of *U. cordatus*, caused by an ascomycete fungus (lethargic crab disease, Boeger et al., 2005; Revista do GIA, 2006), have occurred in 7 of the countries 17 coastal states, particularly in the North-Eastern region (Revista do GIA, 2006). The spreading crab disease has severe impacts on crab populations and consequently fisheries. During a survey of a newly affected area, Schmidt et al. (2004) encountered 52% of the sampled crabs dead and

80% of crab burrows empty. Great concern is given to the question how and how fast populations recover from mass mortality events (Nóbrega and Nishida, 2003; Revista do GIA, 2006; Oliveira-Neto et al., 2007). However, information regarding reproduction and recruitment of *U. cordatus*, in particular larval settlement, is rare. Investigations carried out in the Caeté Estuary (N-Brazil) indicate that *U. cordatus* follows an export strategy (Diele, 2000; Diele and Simith, 2006) with larvae developing offshore at a distance > 60 km (Diele, unpublished). Larval export with extensive gene flow is further indicated by a study on the genetic structure of *U. cordatus* populations in Sergipe and Paraná (Oliveira-Neto et al., 2007). The larvae spend three to four weeks in coastal waters before returning to estuarine waters as megalopae (Diele, 2000). Within the mangrove forest habitat, however, megalopae or first instar crabs have rarely been encountered and it is not known exactly where they naturally settle. Laboratory observations indicated that megalopae and juveniles up to two weeks old preferably burrow at the water-land interface, whereas later stages favour more elevated areas (Diele, 2000; Simith pers. observ.).

Finding a habitat suitable for settlement is a critical step in species with a biphasic life cycle and the transition from the planktonic to the benthic existence is determined by an active larval "decision" (Anger, 2006). Environmental cues characteristic of the adult habitat, e.g. the odour of conspecifics and presence of specific substrata, were shown to trigger metamorphosis to the juvenile stage in many sessile marine species. In the absence of adequate cues they can delay settlement, thereby increasing the chance of finding a suitable habitat elsewhere (review Pechnik 1990, Pawlik, 1992). Compared to the numerous studies on sessile marine invertebrates, in mobile decapods respective studies are scarce (Gebauer et al., 2003). The crab species studied so far also show a capacity for metamorphic delay in the absence of exogenous habitat cues, but over shorter periods and often ending with spontaneous moults (e.g. *Armases roberti:* Anger et al., 2006; *Callinectes sapidus*: Wolcott and de

Vries, 1994; *Chasmagnathus granulata*: Gebauer et al., 1998, 1999; *Panopeus herbstii*: Weber and Epifanio, 1996, Rodriguez and Epifanio, 2000; *Sesarma curacaoense*: Gebauer et al., 2002; *Uca minax:* O´Connor and Judge,2004*; Uca pugilator:* Christy, 1989, O'Connor, 1991; *Uca pugnax:* O'Connor, 1999, O'Connor and Van, 2006).

Due to the biphasic life cycle of *U. coratus* and its off-shore larval advection we presume that habitat choice and settlement of its megalopae is strongly induced by chemical and/or tactile cues from the benthic habitat. We tested this hypothesis by examining the moulting rate and duration of the megalopal phase in the presence and absence of conspecific crab conditioned seawater and different natural and artificial substrata. Natural substrata were collected from the mangrove forest habitat (mud near *Ucides* burrows; dead wood) and also from mid-to lower intertidal areas void of *Ucides* (mud and sand from a tidal channel) within the mangrove estuary. The present study aims to be a first step towards an understanding of pre-metamorphic habitat-selection and settlement in this ecologically and economically important crab. A good understanding of these processes may turn out to be important for the elaboration of future strategies for a rapid recovery of *U. cordatus* stocks in mangrove areas after massive crab mortalities.

2. Materials and methods

2.1. Larval rearing

Seawater for cultivating larvae was obtained 15 to 37 km off the Caeté estuary in N-Brazil (53°09'S, 46°39'W), well behind the estuarine plume, presuming that this water does not induce metamorphosis of *U. cordatus.* The water was filtered (Eheim and Diatom filter, 1µm); sodium chlorate (2.5%) added (2 ml per l seawater) and stored in 500 l tanks with constant aeration. The salinity of the seawater was kept at 30 (by

adding artificial salt or diluting with deionised water) as previous work had shown that the survival of zoea-larvae is highest in high salinity water (Diele and Simith 2006). Larvae were obtained from berried females captured in the mangroves of the Caeté Estuary. The females were kept in 15 l aquaria with filtered offshore water (see above) in the laboratory at the Campus of the Federal University of Pará in Bragança city. To exclude potential effects of extended maintenance in the laboratory, females were only captured the day before their larvae hatched, which was predictable due to the strict lunar rhythm in larval release of *U. cordatus* (Diele 2000). Groups of five larvae were transferred to 150 ml plastic vials and reared to megalopa at constant water temperatures (Cultivation 1: 26.2 ± 0.4 °C; Cultivation 2: 26.0 ± 1.3 °C), salinity 30 and 12 h light / 12 h dark cycle. The larvae were fed daily with freshly hatched *Artemia salina* nauplii and planktonic microalgae (*Dunaliella salina*), both food items known to significantly enhance the survival of cultivated *U. cordatus* larvae (Abrunhosa et al., 2002). The cultivation water was changed every 2 to 4 days. Larvae were checked daily for mortality or moults. Megalopae were kept individually to avoid cannibalism and competition, otherwise they were reared under the same conditions as the zoea larvae.

2.2 Experimental design

Two cultivations were conducted (Table 1). The first cultivation (April 2002) studied the effect of adult conspecifics ("Crab conditioned seawater", TC), naturally occurring substrates ("Channel bank mud", TM; "Sand", TS; "Dead wood", TW; all taken from the Caeté estuary) and artificial substrate ("Nylon mesh", TN) on the moulting frequency and duration of the megalopal phase. Pure seawater served as the control (TSW). All megalopae had the same age and each treatment was conducted with 45 specimens. The experiment was run for 36 days. In the second cultivation (May 2005) the effect of mud collected near adult burrows (TBM) was compared with the effect of TM, TC and the combination of TCM & TC (TCBM). The megalopae used varied in

age (30 to 51 days at day of moulting to megalopa) and were equally distributed between treatments to avoid any effect that differential lengths of the zoea phase may have on the fitness of the megalopae. Each treatment was conducted with 33 specimens and, in contrast to cultivation 1, run until the last megalopae had either moulted to juvenile or died. In both cultivations water and substrates were renewed every 3 to 5 days.

INSERT TABLE 1

2.3 Statistical analysis

Frequency data (% specimens metamorphosed, % megalopae alive, % specimens dead) were analysed by contingency tables (R x C), followed by Chi² tests. After testing for normality (Shapiro-Wilk) and variance homogeneity (Levene), the data on development duration were tested by multiple nonparametric statistics (Kruskall-Wallis), followed by a series of pair wise non-parametric tests (Mann-Whitney). When the moulting rate was zero these data were excluded from the statistical analysis to avoid biasing comparisons between the other treatments.

3. Results

3.1 Cultivation 1

The number of megalopae that metamorphosed to juvenile crab during the 36 days of the experiment varied significantly between treatments ($p < 0.0001$). In TC 89 % of the initial 45 megalopae reached the juvenile stage, in TM the second highest metamorphosis rate occurred (67 %), while less than 20 % of the megalopae metamorphosed in the remaining treatments (Fig. 1a).

In TC all specimens had either reached the juvenile phase or had died by day 36. In the remaining treatments, there were still megalopae alive at the end of the cultivation (Fig. 1b). Numbers differed significantly ($p < 0.0001$): In TM only 9% of the specimens were still in the megalopal phase, while 7 (TW) to 10 fold (TSW) higher numbers occurred in the remaining four treatments (Fig. 1b). The number of specimens that had died until the end of the cultivation ranged between 7 % in TSW and 24 % in TM and TW (Fig. 1c).

INSERT FIGURE 1

The duration of the megalopal phase of the specimens that had metamorphosed to juvenile within the 36 cultivation days ranged between 11 and 31 days and differed significantly between TC and the rest of the treatments (Fig. 2) ($p < 0.0001$). In TC, the average duration of the megalopal phase was shortest (13.1 ± 0.37 days). Between the remaining treatments differences were not significant, their average duration was 7 days longer than in TC (20.72 ± 5.23, pooled data) (Fig. 2). Large differences between TC and the other treatments also occurred concerning the timing of metamorphosis. In the former an abrupt onset of moulting to juvenile occurred on day 11, when 40% of all specimens had metamorphosed (Fig. 3). By day 13, over 50% of the megalopae in TC had reached the juvenile stage, while no more than 2 and 4% had metamorphosed in the other treatments by this time. By day 17, all megalopae that moulted within the 36 days of the cultivation had reached the juvenile phase in TC, whereas in the other treatments most moulting events occurred after day 17 (except in TS). In TM 50% of all megalopae had moulted by day 22. On day 31 the last moults occurred in TM, TW and TSW. During the final 4 days of the experiment no more megalopae metamorphosed, even though many specimens were still alive.

INSERT FIGURE 2

INSERT FIGURE 3

3.2 Cultivation 2

Unlike cultivation 1, cultivation 2 was performed until the last megalopa in each treatment had metamorphosed or died. In the seawater control, TSW, all megalopae died without having reached the benthic phase. In the other four treatments (TCBM, TC, TBM and TM, see figure 4), the rate of metamorphosis and thus survival was high: between 91 and 70 % of the megalopae reached the juvenile stage. The moulting rate did not differ statistically between TCBM, TC and TBM, but significantly more specimens moulted to crab in TCBM than in TM (22 %, $p < 0.05$). In TC the metamorphosis rate was still 18 % higher than in TM, but statistically insignificant. TBM and TM were also similar.

INSERT FIGURE 4

The duration of the megalopal phase of the metamorphosed specimens ranged between 6 and 32 days and differed significantly between treatments ($p < 0.0001$). The shortest average values were observed in TCBM (12.80 ± 2.66 days) and in TC (13.62 ± 2.73), while the longest megalopal period occurred in TM (20.3 ± 5.69 days).

INSERT FIGURE 5

In most treatments the first juveniles appeared on day 9 and 10 (Fig. 6). Moulting events then increased steeply in TCBM, TC and TBM and by day 13, 14 and 16, respectively, more than 50% of the specimens had reached the juvenile phase. In TM the increase in metamorphosis events took place more gradually and 50% was only

reached on day 24. After day 32 no more megalopae metamorphosed. In TBM the last specimens died on day 33, in TM on day 37 and in the sea water control approx. 2 months after the onset of the megalopal phase.

INSERT FIGURE 6

The outcomes of cultivation 1 and 2 for the repeated treatments TC, TM and TSW were similar, even though the larvae were derived from different females and in different years. The difference in percentage of metamorphosed megalopae between the two cultivations was 1% for TC, 3% for TM and 4 % for TSW (Fig. 1, Fig. 4). Average development duration of TC and TM varied by less than a day (Fig. 2, Fig. 5) and the day at which at least 50% of the larvae had metamorphosed also only differed by one (TC) or two days (TM) between the two cultivations (Fig.3, Fig. 6). Possible intraspecific variations in genetic and / or maternal factors and experimental variations did thus not have a large effect.

4. Discussion

In several brachyuran crabs environmental cues from the adult habitat influence the settlement of their final larval stage (review by Anger, 2001; Forward et al. 2001; Gebauer et al., 2003). The present study is the first to show that this is also true for the mangrove crab *Ucides cordatus*. Specific cues associated with the habitat of the benthic phase of its life cycle affected both the rate of metamorphosis and the duration of the megalopal phase.

The odour of conspecific crabs (crab conditioned seawater) as well as mud (taken near crab burrows and from the channel-bank) were strong inducers of metamorphosis in *U. cordatus* megalopae. The megalopae responded to these

treatments by 4 to 5 fold higher moulting rates compared with dead wood taken from the mangrove forest, sand from tidal flats and the control seawater treatment. The number of megalopae moulting to juvenile over sand and dead wood was similarly low as in the treatment with artificial substrate (nylon mesh). This also underlines that the two former substrates are not perceived as reliable habitat indicators, despite their abundance in the forest and estuarine habitat.

Our laboratory results suggest that *U. cordatus* megalopae settle in areas populated by conspecific crabs and /or in muddy habitats. Whereas hardly any larvae moulted to juvenile in the seawater control treatment (4 and 0% in cultivation 1 and 2, respectively), high moulting rates above 80% occurred in crab conditioned seawater (TC). This demonstrates that megalopae do not necessarily need tactile cues for their settlement. Instead, water-borne cues alone, such as adult odour, can induce metamorphosis. Moulting rates above 80% were also observed in the combined treatment of crab-conditioned seawater and burrow mud (TCBM). Furthermore, high numbers of megalopae metamorphosed over burrow mud alone (TBM, 76%) as well as over channel-bank mud (TM, 67 and 70% in cultivation 1 and 2, respectively). The latter suggests that *Ucides* megalopae may also settle in muddy habitats where conspecific crabs are not directly nearby. A tactile sediment characteristic could be responsible for the metamorphic response, but it is also possible that the mud taken from the channel-bank may have contained chemical substances emitted by *Ucides* (e.g. pheromones, ammonium), despite the absence of conspecifics within the next 15 to 20 m. For fiddler crabs O'Connor (1991) and O'Connor and Van (2006) discussed and showed that sediments may retain chemical cues released by conspecifics crabs, and consequently stimulate moulting of fiddler crab megalopae, rather than the sediments themselves. Odour concentrations of *U. cordatus* are likely to be high in our study area, which comprises 140 km² of densely populated mangroves with > 230 millions of crabs (extrapolated from Diele et al. 2005). Ebb tides may carry these

water-soluble chemical cues from the inner forest to bank sediments and microbial biofilms could be responsible for binding such allochthonous substances to sediment surfaces (Decho, 1990; Weber and Epifanio, 1996; Rodriguez and Epifanio, 2000; O'Connor and Van, 2006). Whether *Ucides* megalopae respond to conspecific odour molecules absorbed by such biofilms or whether biofilms themselves produce a settlement inducing substance, e.g. microbial exopolymers, remains unclear.

In addition to provoking a high moulting rate, conspecific odour also significantly reduced the length of the megalopal phase in *U. cordatus*. In TC the average duration of this phase was up to 8 days (38 %), in TCBM 7 days (37%) and in TBM still 4 days (21%) shorter than in TM, indicating that megalopae are capable of actively modulating the timing of metamorphosis in response to environmental cues. This capacity involves both benefits and costs. The obvious benefit for a species such as *U. cordatus* with larvae developing offshore (Diele 2000; Diele & Simith 2006; Diele unpubl.) is that metamorphosis to juvenile can be delayed in the absence of a suitable habitat. A continued larval drift increases the chance for finding an adequate place for settlement elsewhere (Anger, 2006). On the other hand a prolonged larval phase also enhances the risk of mortality, e.g. by pelagic predators and by advection (Morgan, 1995; Eckert, 2003). A further trade-off of delayed metamorphosis involves carry-over effects (sensu Anger, 2006) of larval condition on postmetamorphic fitness. For example, in *Chasmagnathus granulata* delayed metamorphosis resulted in reduced body size, survival and growth in first juveniles and these specimens also remained smaller and moulted later throughout successive juvenile instars (Gebauer et al., 1999). A smaller size may increase vulnerability to benthic predation and decrease individual competitive strength (review Gebauer et al., 2003). Hence, while different environmental cues or cue combinations may be very effective in triggering metamorphosis (TC, TCBM, TBM, TM), they may still have a differential effect on the fitness of the benthic stages and population dynamics of a species, by their varying

impact on the duration of larval development. Further studies are planned to investigate how *U. cordatus* reacts to delayed metamorphosis regarding initial juvenile size, growth and survival.

Only two megalopae moulted to juvenile in the seawater control in the first cultivation, with a delay of 13 days compared with specimens reared in contact with crab-conditioned water. In the second experiment all megalopae died prior to metamorphosis. In contrast, in *Chasmagnathus granulata* (Gebauer et al., 1998) more than 50% of the megalopae reared in seawater survived to juvenile, and metamorphosis was delayed by about 3 days only. Gebauer et al. (1998) suggest that selection favours a relatively short period of metamorphic competence rather than a longer one that would reduce juvenile fitness. In *U. cordatus,* however, the almost complete absence of spontaneous moulting events in seawater indicates that the selective advantage of delaying metamorphosis, namely the chance for finding a favourable habitat through continued drift, is larger than when metamorphosing in an unsuitable area where the chance of survival of the post-metamorphic stages is null. The relatively unspecific metamorphic response in *C. granulata* compared to the strict dependence in *U. cordatus* might result from a lower degree of habitat specialization. While the latter species is exclusively found in mangrove forests, the former densely populates mudflats bare of vegetation as well as salt marshes in estuaries, bays and coastal lagoons of varying salinities, temperatures and tidal patterns (Bas et al., 2005).

U. cordatus megalopae strongly responded towards the odour of conspecifics, but we do not yet know whether the chemical cue responsible is species-specific or if *Ucides* megalopae would also react to the odour of other crab species. The latter was observed for *Sesarma curacaoense* (Gebauer et al., 2002), where metamorphosis was also significantly accelerated by closely related species, suggesting a similar

chemical structure of their odour and the one of conspecifics. *U. cordatus* co-occurs with several other estuarine ocypodid crabs (Uca sp.) and possibly their odour also induces metamorphosis in *Ucides* megalopae. For example, the high settlement rate in TM could have been provoked by chemical cues of *Uca maracoani* that burrow in the channel bank, instead of *Ucides* odour originating from the forest habitat (or alternatively settlement inducing cues produced by microbial biofilms, as suggested above). The question whether larval settlement is promoted by conspecific odour only or also by co-occurring species is of particular importance in *U. cordatus* against the background of the spreading lethargic crab disease (LCD). This fungal disease strongly affects *Ucides*, (Boeger et al.,2005), while *Uca* sp. have not been observed with clinical signs (Boeger, personal communication). If the presence of the apparently immune fiddler crabs significantly enhances settlement of *U. cordatus* megalopae, it would accelerate the re-establishment of viable *Ucides* populations in areas affected by LCD. In contrast, if settlement was primarily induced by conspecific crabs, re-population after *Ucides* mass mortalities would be retarded. In future studies we will look more closely at the origin and the molecular structure of the settlement inducing substances for a better understanding of the role of intra- and interspecific cues.

In summary, we now know that habitat characteristic chemical cues trigger the settlement of *U. cordatus* megalopae in mangrove estuaries and that the larvae die before settling when these cues are absent. The presence of adequate habitat-indicators thus plays a crucial role for recruitment and consequently for the establishment and maintenance of viable populations of this ecologically and economically important species.

5. Acknowledgements

6. References

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Tables

Table 1. Description of treatments run during the first (C1) and second cultivation (C2).

Treatment	C1	C2	Description
TC	x	x	*"Crab conditioned seawater"* An adult conspecific female (carapace width 5.98 and 5.35 cm in C1 and C2, respectively) was freshly collected, rinsed and submersed for 24 hrs in 10l of seawater. The crab was then removed and the water sieved (100 μm) to remove setae and other organic matter.
TM	x	x	*"Channel bank mud"* The upper 2-3 cm of surface sediment was collected at low tide from the mid-intertidal region of the bank of a large tidal channel, an area where *U. cordatus* does not burrow within the next 15 to 20 m. 4 to 6 g fresh surface sediment was added to the cultivation vial and distributed homogenously on its bottom.
TS	x	-	*"Sand"* The bottom of the cultivation vial was covered with approx. 5 mm of sand taken from the surface of an intertidal sand flat. The latter was located within the same tidal channel from which mud for TM was obtained.
TW	x	-	*"Dead Wood"* An approx. 2 cm piece of dead *Rhizophora mangle* wood collected from the ground of a mangrove forest with abundant *U. cordatus*, was added
TN	x	-	*"Nylon mesh"* A 2x2 cm piece of 500 μm nylon mesh was put on the bottom of the cultivation floor
TBM	-	x	*"Burrow mud"* Surface sediment up to a depth of 2-3 cm was collected near the openings of adult burrows in a forest area with abundant *U. cordatus*. 4 to 6 g of this sediment was added to the cultivation vial and distributed homogenously on its bottom.
TCBM	-	x	*"Crab conditioned seawater / Burrow mud"* TC and TBM combined
TSW	x	x	"Seawater control", see 2.1

Figure Captures

Figure 1. Percentage of metamorphosed *U. cordatus* megalopae (1a), alive megalopae (1b) and dead megalopae (1c) in different water and substrate treatments (for abbreviations see Table 1) at the end of cultivation 1. Equal letters indicate statistically homogeneous groups (p > 0.05).

Figure 2. Average duration (± 1 SD) of the megalopal phase of *U. cordatus* in different water and substrate treatments in cultivation 1 (see Table 1 for abbreviations). Equal letters indicate statistically homogeneous groups (p > 0.05). Numbers in bars indicate the number of specimens that metamorphosed.

Figure 3. Cumulative percentage of metamorphosed *U. cordatus* megalopae in different water and substrate treatments (see Table 1 for abbreviations) in cultivation 1. Dashed line indicates 50%.

Figure 4. Percentage of metamorphosed *U. cordatus* megalopae in different water and substrate treatments (for abbreviations see Table 1) at the end of cultivation 2. Equal letters indicate statistically homogeneous groups (p > 0.05).

Figure 5. Average duration (± 1 SD) of the megalopal phase of *U. cordatus* in different water and substrate treatments (see Table 1 for abbreviations) in cultivation 2. Equal letters indicate statistically homogeneous groups (p > 0.05). Numbers in bars indicate the number of specimens that metamorphosed during the experiment.

Figure 6. Cumulative percentage of metamorphosed *U. cordatus* megalopae in different water and substrate treatments (see Table 1 for abbreviations) in cultivation 2. Dashed line indicates 50%.
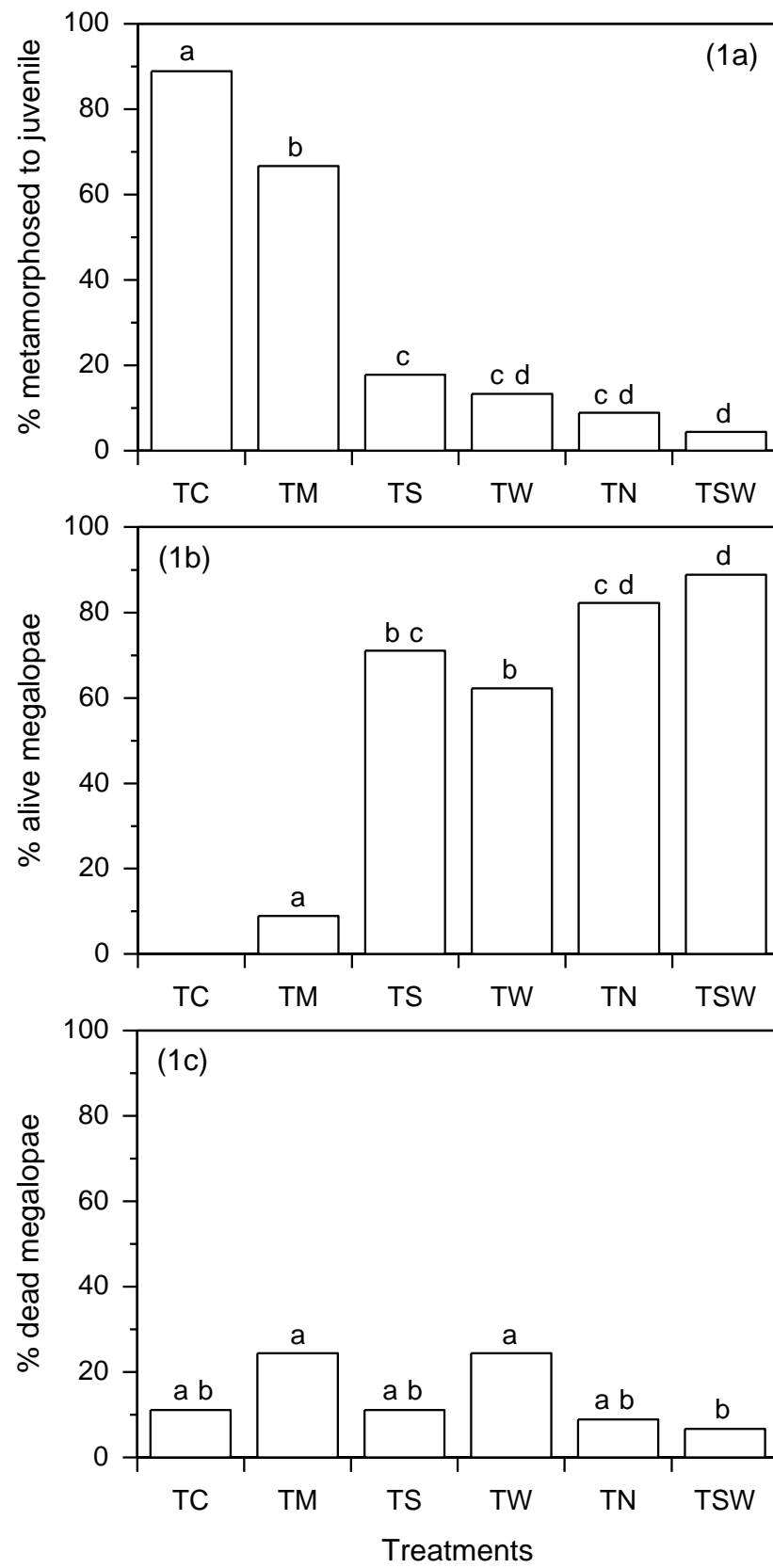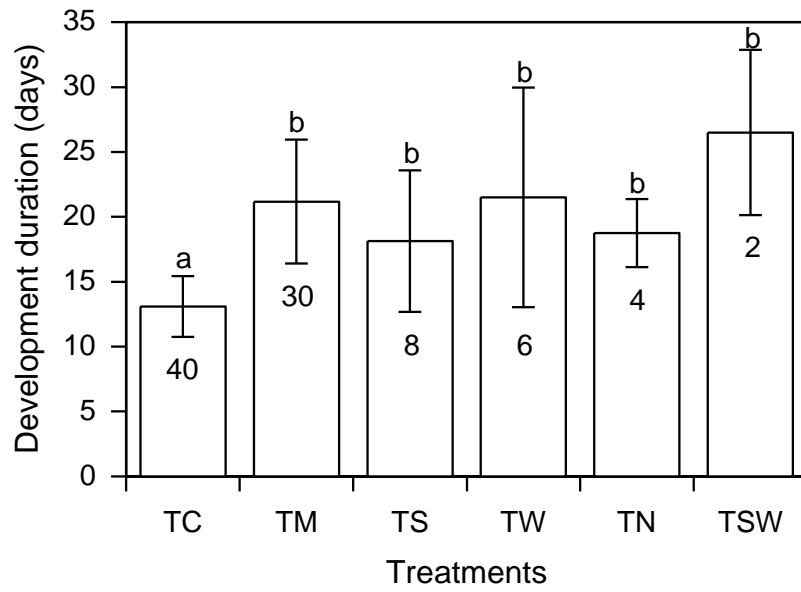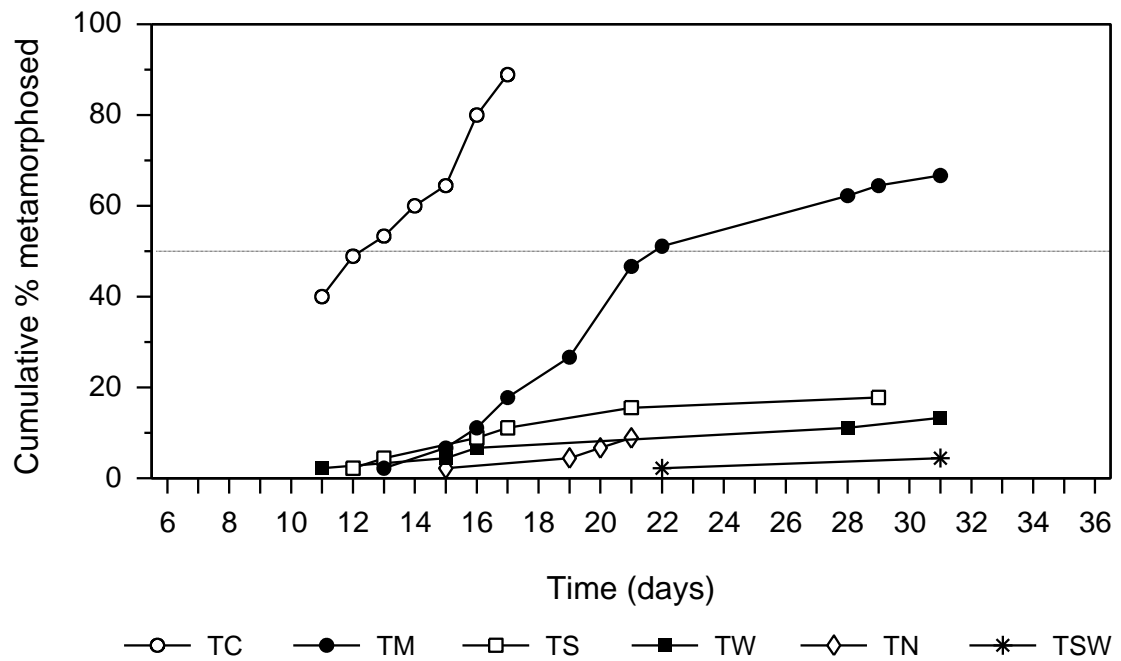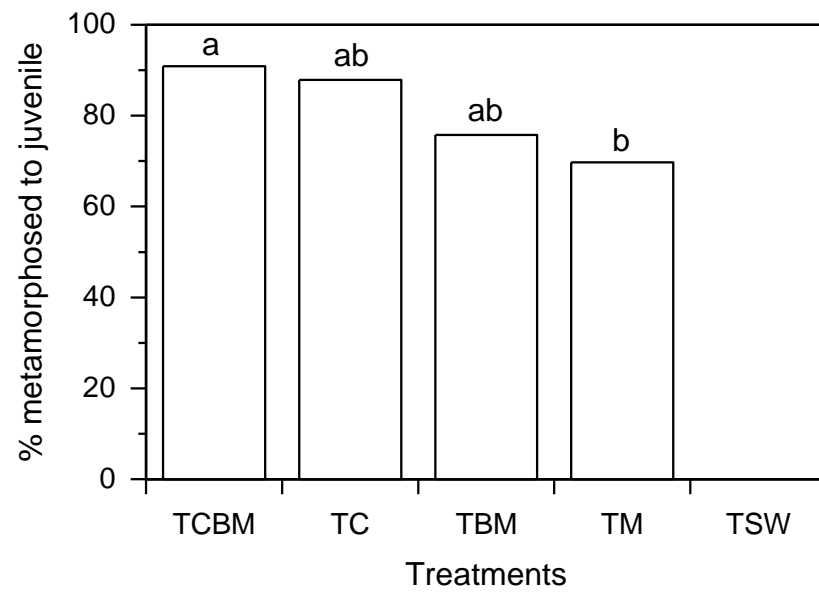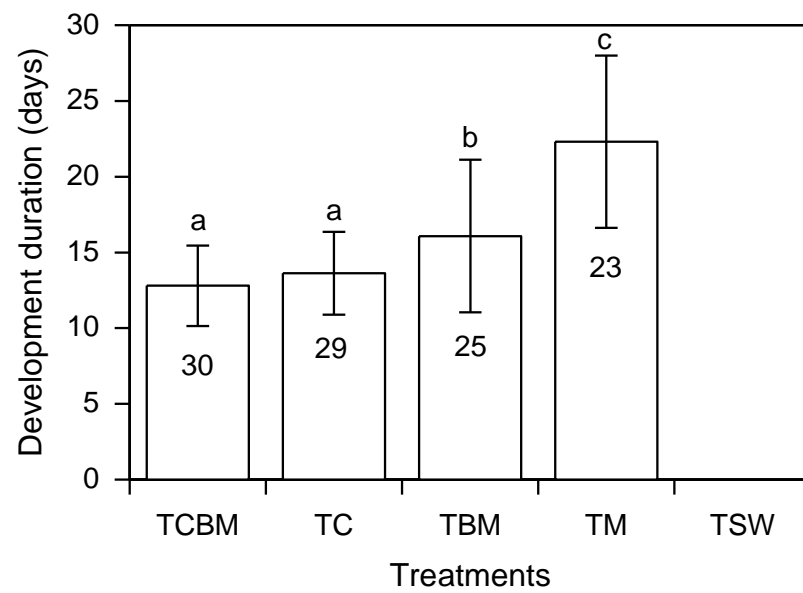
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6