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Effects of substratum and conspecific adults on the development and metamorphosis of *Acanthocyclus hassleri* (Brachyura: Bellidae) megalopae under laboratory conditions

Efecto del sustrato y adultos conespecíficos sobre el desarrollo y metamorfosis de megalopas de *Acanthocyclus hassleri* (Brachyura: Bellidae) bajo condiciones de laboratorio

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Resumen.- El éxito en la transición pélogo-bentónica del meroplankton depende en gran medida de las señales ambientales que induzcan el asentamiento y la metamorfosis. *Acanthocyclus hassleri* interactúa con las colonias sésiles de *Perumytilus purpuratus* y *Phragmatopoma virgini* desde etapas ontogenéticas tempranas; por ello planteamos que el desarrollo y la metamorfosis de la megalopa de *A. hassleri* son influenciadas por la presencia de estas especies y/o adultos conespecíficos. Evaluamos el tiempo de desarrollo, frecuencia de metamorfoseados y supervivencia de megalopas en cultivo, usando como sustratos *P. purpuratus*, *P. virgini*, conchas y habitáculos vacíos de ambas especies, un tratamiento con agua de adultos conespecíficos y un control sin estímulo. El desarrollo megalopal fue significativamente más corto en los tratamientos con sustrato. En promedio, el retardo de la metamorfosis fue de cuatro días. La mortalidad fue levemente menor en los tratamientos sin sustrato, pero sin diferencias significativas. El desarrollo de la megalopa está influenciado por las condiciones físicas del sustrato, no así la supervivencia, ya que la larva metamorfosea espontáneamente en ausencia de estímulo. El retardo de la metamorfosis es menor que en otras especies; además, la temperatura de cultivo fue menor a su óptimo térmico, por lo que este umbral puede ser aún mas estrecho en condiciones cercanas al óptimo. Comparando nuestros resultados con estudios en especies estuarinas y gregarias, se sugiere que la naturaleza del estímulo y la respuesta larval puede depender de la densidad poblacional adulta y la energía involucrada en la hidrodinámica del hábitat.

Palabras clave: Decapoda, larva, inducción, señal ambiental, transición pélogo-bentónica

Abstract.- Success in the pelagic-benthic transition of the meroplankton depends to a great extent on the environmental signals that induce the settlement and metamorphosis. *Acanthocyclus hassleri* interacts with sessile colonies of *Perumytilus purpuratus* and *Phragmatopoma virgini* from its early ontogenetic stages onwards. Thus, we propose that megalopal development and metamorphosis of *A. hassleri* are influenced by the presence of such species and/or conspecific adults. We evaluated the development time, frequency of metamorphosis, and survival of megalopae in culture, using as substrates *P. purpuratus*, *P. virgini*, empty shells and dwellings of both species, a treatment with water exposed to conspecific adults, and a control experiment without stimulus. Megalopal development was significantly shorter in treatments with a substrate. The average delay in metamorphosis was four days. Mortality was slightly lower in treatments without a substrate, but this was not statistically significant. Megalopal development was influenced by the physical conditions of the substrate, but not the survival because the larvae metamorphosed spontaneously in the absence of stimulation. Delay in metamorphosis was lower than in other species; furthermore, the temperature of the culture was lower than the thermal optimum, thus it is likely that this threshold would be even narrower under conditions closer to the optimum. Comparing our results with studies in estuarine and gregarious species, we suggested that the nature of stimulus and larval response could depend on the population density of the adults and the energy involved in the hydrodynamics of habitat.

Key words: Decapoda, larvae, induction, environmental cue, pelagic-benthic transition

INTRODUCTION

Benthic marine invertebrates with meroplanktonic life cycles are characterized by to have pelagic larval phases followed by a benthic adult stage. Transition between both

environments involves three processes closely related and widely discussed, *i.e.*, settlement, metamorphosis, and recruitment (Chia 1978, Pechenik 2006). Settlement

includes behavioral patterns of sinking through the water column and the search for certain features on the substrate that induce the morphological, physiological and metabolic changes involved in metamorphosis and adaptation to new habitat (Hadfield 1986, Rodríguez *et al.* 1993). On the other hand, recruitment is defined in simple terms as the incorporation of new members into a population by reproduction or immigration (Lincoln *et al.* 1998). However, for others this concept is related to survival and/or the period required for newly settled individuals reach a certain size (*e.g.*, Roegner 1991). Despite the conceptual variations, it is possible to generalize that the settlement and metamorphosis are explained by mechanisms operating at the individual level (*e.g.*, behavior patterns, physiological responses), while recruitment depends on density-dependent processes arising from population dynamics (Hurlbut 1991, Anger 2001, Pardo *et al.* 2007).

Throughout larval ontogeny, there are different critical points in development that are controlled by the interaction between extrinsic factors such as temperature, salinity, food availability, and intrinsic factors such as endocrine regulation or the genetic basis of various organismic processes (Anger 1987, Olson & Olson 1989). In particular, in the settlement and metamorphosis processes there are active interactions between the individual and the environment involved. Premetamorphic stages of most benthic marine invertebrates are characterized by a specific adaptive condition known as metamorphic competence or a competent larval stage (Hadfield 2000). In this phase, different environmental features can act as signals that the larvae are able to detect and associate with information on habitat quality necessary for the development of postmetamorphic juveniles (Hadfield *et al.* 2001). In this context, there occur two types of mutually exclusive responses: (a) the environmental cues captured by the competent larva induce the sequence of events involved in metamorphosis, or (b) in the absence of an appropriate environmental cue, the competent larvae delay metamorphosis within a certain time threshold, after which spontaneous metamorphosis or the death of the competent larva occurs (Pawlik 1998, Pechenik *et al.* 1998).

The larval stage that precedes the metamorphosis and transformation to first juvenile in many decapod crustaceans is the megalopa (Williamson 1969). Morphofunctionally, the megalopa is able to swim in the water column using its pleopods and walk on the bottom using its pereopods. Thus, the megalopa is responsible for the pelagic-benthic transition and consequently, it must achieve metamorphic competence, before passing through

settlement and metamorphosis (McConaughy 1992, Anger 2001). Several studies have reported that both the duration and survival of megalopa stage as body size and growth of postmetamorphic individuals may be strongly influenced by the presence or absence of physical and/or chemical cues from the habitat of the adult population. Many stimuli have been experimentally tested to determine if they function as inducers of settlement and metamorphosis in decapod megalopae. For example, the manipulation of variables associated with the environmental dynamics of estuaries, such as reducing salinity or the presence of humic acid accelerated the metamorphosis in the crab *Callinectes sapidus* (Forward *et al.* 1997). In addition, different types of substrate also generate variability in the development time of megalopae and postmetamorphic survival in *Uca pugilator* and *Neohelice* (= *Chasmagnathus*) *granulata* (Christy 1989, Gebauer *et al.* 1998). On the other hand, the presence of adults and/or excretion products from conspecifics or phylogenetically related individuals have been reported as potential metamorphic inducers in *U. pugnax*, *N. granulata* and *Sesarma curacaoense* amongst other species (O'Connor & Gregg 1998, Gebauer *et al.* 1998, 2002, 2003).

The *Acanthocyclus* genus is a taxon of brachyuran crabs composed of three species, *A. hassleri*, *A. albatrossis*, and *A. gayi* which inhabit the rocky intertidal zone along the majority of the of Chilean coast (Zagal *et al.* 2001). Of the three species, *A. hassleri* has the widest latitudinal distribution and higher population abundances on the coast of the Valdivia province (Retamal 1981, Carrasco & Zamorano 2000). This species is also an important regulator of the population and topographical structure of the most abundant sessile organisms of the intertidal of southern-central Chile.

The regulated species include the mussel *Perumytilus purpuratus* and the reef-forming sabellarid polychaete *Phragmathopoma virgini* (Castilla *et al.* 1989, Zamorano *et al.* 1995), both of which also play important ecological roles as bioengineers and facilitators of microhabitats for a significant portion of the invertebrate community in these areas (Sepúlveda *et al.* 2003, Prado & Castilla 2006). Taking account that *Acanthocyclus* species recruit to the intertidal zone, maintaining a close interaction with the colonies of *P. purpuratus* and *P. virgini* from early postlarval ontogeny (Jara & Moreno 1983, Navarrete *et al.* 2008), and that *A. hassleri* have a relatively higher density with respect of their congeneric species, it is plausible that both the colonial species and/or conspecifics adults may act as potential promoters of settlement and

metamorphosis for this crab. We hypothesized that exposure to potential inducers of settlement and metamorphosis, present on the substrate or dissolved in the water, generate different effects on the development and survival of *A. hassleri* megalopae. Therefore, the objective of this study was to compare the development time and success of the metamorphosis of *A. hassleri* megalopae by exposing them experimentally to products of the excretion of conspecific adults and the main biogenic substrates with which this species interacts on the southern-central Chilean coast.

MATERIAL AND METHODS

Ovigerous females of *Acanthocyclos hassleri* were collected by hand at low tide from the rocky intertidal zone at Pichicullín in the Valdivia province, south-central Chile (39°25'S, 73°13'W). The individuals were transported live to the Institute of Zoology of the Universidad Austral de Chile. Females carrying eggs at an advanced stage of embryonic development were selected. This was determined primarily by the presence of eyespots, development of the abdomen and appendages, the observation of internal movements, heartbeat, and low percentage of yolk remaining (Wehrmann & López 2003). The selected females were maintained in glass aquaria in 500 ml of filtered seawater (pore size 1 µm and UV irradiated) with constant aeration until the larvae hatched. The maintenance of ovigerous females, the cultivation of zoea larvae and the experiments with megalopae were all conducted under temperature, salinity, and photoperiod conditions of 12°C, 33±1‰, and 12:12 h light:dark, respectively.

Five females began to release larvae 72 h after their arrival in the laboratory. Zoea cultures were started with larvae that were produced on the second day after hatching began. The cultures were maintained in 500 ml plastic containers each holding 400 ml seawater, with an initial population of 100 zoeae per container. Seawater used for culturing was passed through a series of filters of 10 µm, 5 µm, 1 µm, 0.5 µm and ultraviolet radiation. The culture seawater and vessels were changed daily. Larvae were fed daily *ad libitum* with recently hatched *Artemia* sp. nauplii. Under these conditions we reared 1500 zoea from five females randomly distributed across 15 containers.

To assess how the development of the megalopa and metamorphosis success rates of *A. hassleri* were influenced by different environmental cues, 540 newly molted megalopae were distributed across six experimental

treatments: 1) living individuals of *Perumytilus purpuratus* (Pp); 2) living individuals of *Phragmatopoma virgini* (Pv); 3) empty shells of *P. purpuratus* (s-Pp); 4) empty dwellings of *P. virgini* (d-Pv); 5) water previously incubated with conspecific adults (CA); and 6) a control treatment consisting of sea water filtered and then sterilized with ultraviolet radiation (Co). In each experimental treatment we used nine replicates, each consisting of a 350 ml plastic bowl containing the specified substrate and 10 newly molted megalopae. In treatments Pp and Pv, aggregations of 12 individuals of either *P. purpuratus* or *P. virgini* were selected. Each aggregation was carefully cleaned under a Wild M3Z stereomicroscope ensuring the total removal of epibionts. For treatments s-Pp and d-Pv, aggregations of a similar number of individuals were boiled in distilled water and all the soft tissues removed.

The duration of the megalopal stage was measured as the period of time (in days) between the moult to megalopa and the metamorphosis to first juvenile. In addition, for each treatment, we calculated the cumulative frequency of metamorphosis in time. With this information, and following the analysis developed by Gebauer *et al.* (1998), we compared the percentage of individuals metamorphosed at two specific points during the experiments: 1) when metamorphosis was achieved by 50% of megalopae belonging to a treatment with a shorter development time, and 2) when metamorphosis was achieved by 50% of the individuals in the treatment with the highest megalopal development time. Finally, metamorphic success was reflected by megalopal survival, defined as the percentage of individuals that achieved metamorphosis.

All data were subjected to the Shapiro-Wilks normality test (Gill 1978) and the Brown-Forsythe homoscedasticity test (Brown & Forsythe 1974). If the data did not meet the assumptions required for parametric hypothesis testing, a logarithmic transformation of megalopal development time and an angular transformation for all percentage data were performed. If data were parametric, we applied a one-way ANOVA with *a posteriori* Tuckey test of least significant difference; otherwise, a nonparametric Kruskal-Wallis hypothesis test was performed (Zar 1999).

RESULTS

Larval development of *A. hassleri* consists of four zoeal phases and one megalopal stage. The total zoeal stage lasted on average 72 ± 3.6 days, with a survival of approximately 79% at the end of the Zoea IV stage. Therefore, from the initial population (1500 newly hatched

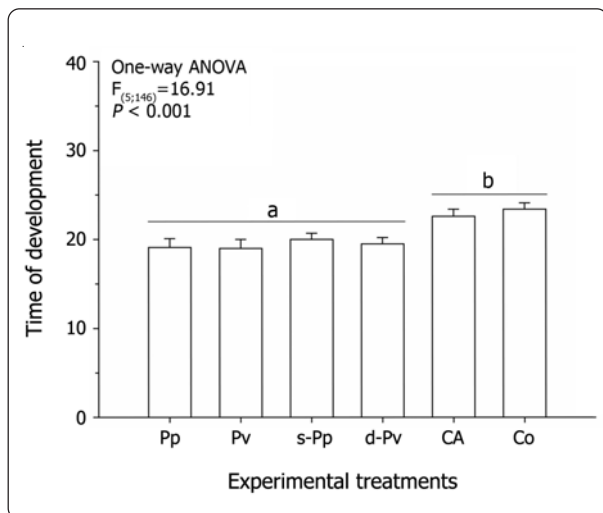


Figure 1. Development time (mean \pm standard deviation) of *A. hassleri* megalopae exposed to different treatments designed to induce metamorphosis (Pp: *P. purpuratus*, Pv: *P. virgini*, s-Pp: empty shells of *P. purpuratus*, d-Pv: empty dwellings of *P. virgini*, CA: water incubated with conspecific adults, and Co: control treatment) Lower-case letters indicate statistically significant differences / Tiempo de desarrollo (promedio \pm desviación estándar) en megalopas de *A. hassleri* expuestas a diferentes tratamientos de inducción a la metamorfosis. (Pp: *P. purpuratus*, Pv: *P. virgini*, s-Pp: conchas vacías de *P. purpuratus*, d-Pv: hábitáculos vacíos de *P. virgini*, CA: agua incubada con adultos conspecíficos y Co: tratamiento control). Las letras minúsculas indican diferencias estadísticamente significativas

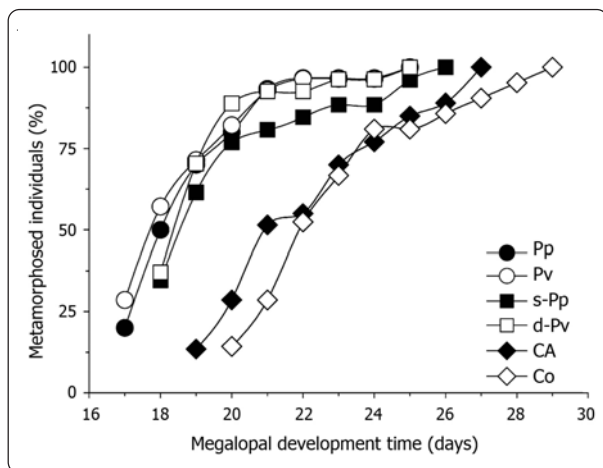


Figure 2. Cumulative percentage curves for the time of metamorphosed individuals of *A. hassleri* experimentally subjected to different treatments designed to induce metamorphosis. Abbreviations as in Fig. 1 / Curvas de porcentaje acumulado en el tiempo de individuos metamorfoseados de *A. hassleri* sometidos experimentalmente a diferentes tratamientos de inducción a la metamorfosis. Abreviaciones como en la Fig. 1

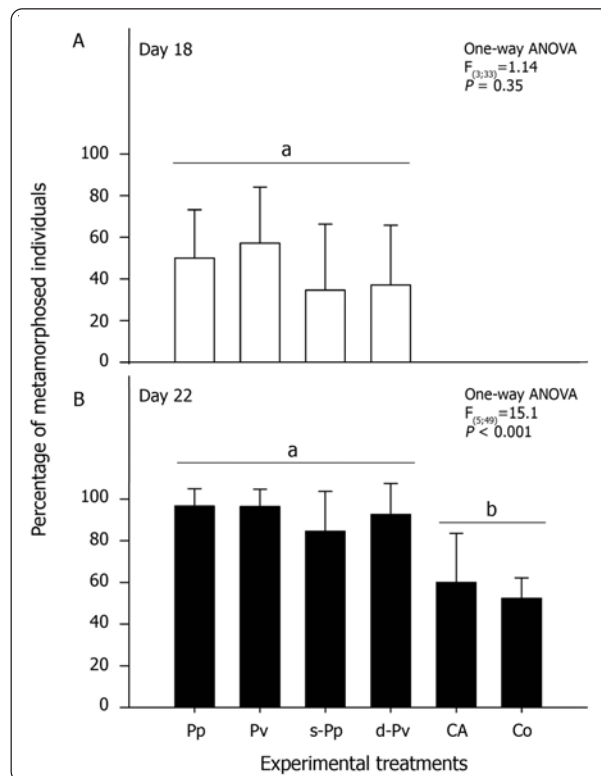


Figure 3. Percentage of metamorphosed larvae (mean \pm standard deviation) in each treatment in two times within of the experiment: A) when 50% of individuals from the treatment with the most rapid metamorphosis moulted to first juvenile (day 18), and B) when at least half of the individuals had metamorphosed in all treatments (day 22). Abbreviations as in Fig. 1. Lower-case letters indicate statistically significant differences / Porcentaje de larvas metamorfoseadas (promedio \pm desviación estándar) para cada tratamiento en dos momentos dentro del experimento: A) cuando el 50% de los individuos del tratamiento más rápido mudó a primer juvenil (día 18) y B) cuando al menos la mitad de los individuos metamorfoseó en todos los tratamientos (día 22). Abreviaciones como en la Fig. 1. Las letras minúsculas indican diferencias estadísticamente significativas

larvae), 1200 individuals completed the zoal stage, the first 540 newly molted megalopae were selected for the experiments.

The duration of the megalopal stage was significantly higher in the control and water incubated with conspecific adults treatments compared to that observed in the other treatments, which on average did not exceed 20 days of development (Fig. 1).

In those treatments that used living individuals of *Perumytilus purpuratus* and *Phragmatopoma virgini* as substrates, 50% of the megalopae had reached metamorphosis at 18 days of development (Fig. 2, 3A). By contrast, in water incubated with conspecific adults

and the control, half of the larvae had metamorphosed at 20 and 22 days of development, respectively (Fig. 2, 3B), with no metamorphosis having taken place by day 18 of development in this treatments. At 18 days of development, the percentage of metamorphosed larvae exhibited non significant differences between the four treatments with substrates. On the other hand, at 22 days of development, the percentage of metamorphosed individuals was significantly higher in the four experimental treatments with substrates compared to the water incubated with conspecific adults and control treatments (Fig. 3A, B).

Survival varied on average between 22.2% and 33.3%. At the time at which all existing megalopae metamorphosed to first juvenile, the treatments of water incubated with conspecific adults and control had lower survival rates than the treatments with substrates; however, these differences were not statistically significant (Fig. 4).

DISCUSSION

Compared with previous results (Barría *et al.* 2005), the development time and survival of the zoeae were within the range expected under the thermal conditions of this experiment. This indicates that the method of cultivation had no effect on larval ontogeny that might bias the experimental responses. Thus, the results partially support the hypothesis, given that the environmental stimuli tested significantly affected the duration of the megalopa stage, but not the survival of individuals metamorphosed.

All substrates significantly reduced development time, but there were no differential effects caused by using living organisms or their hard structures as metamorphic inducers. This indicates that in *A. hassleri*, the metamorphosis is not affected by chemical cues from substrates or by conspecific adults. Therefore, under this experimental design, the main metamorphic inducers in the competent larvae of *A. hassleri* came from the physical characteristics of substrate.

Our results contrast with those reported for other brachyuran species. For example, in the grapsid crab *N. granulata*, the presence of mud in combination with chemical factors from conspecific adults reduced the megalopal development time, accelerating metamorphosis (Gebauer *et al.* 1998). A similar response was found in *S. curacaoense*, where the metamorphosis was stimulated to varying degrees by factors from chemical substances secreted by conspecific and phylogenetically related species (Gebauer *et al.* 2002). Both species are gregarious and inhabit muddy marshes, coastal lagoons, and estuaries

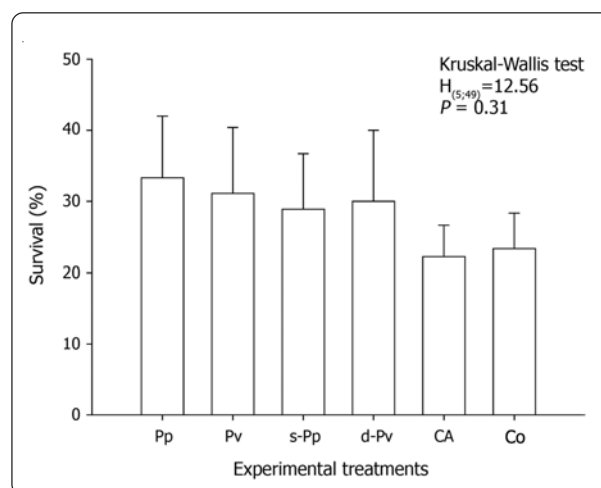


Figure 4. Survival at metamorphosis of *A. hassleri* megalopae exposed to different treatments designed to induce metamorphosis. Abbreviations as in Fig. 1 / Supervivencia en la metamorfosis de las megalopas de *A. hassleri* expuestas a diferentes tratamientos de inducción a la metamorfosis. Abreviaciones como en la Fig. 1

in the case of *N. granulata* (Boschi 1964, Spivak 2010) and the shallow waters of mangroves in the case of *S. curacaoense* (Abele 1992). These environments are characterized by low energy hydrographic dynamics, as they are mainly influenced by tidal regimes (Hayes 1979). On the other hand, the *Acanthocyclus* genus recruits in the intertidal zone of exposed rocky shores (Jara & Moreno 1983, Castilla *et al.* 1989), whose dynamics are influenced by wave action and high velocity energetic current. This creates a heterogeneous mosaic of hydrodynamic conditions that influence the patterns of coastal advection of benthic invertebrate larvae (Palma *et al.* 2006). Under these conditions, the textural and microtopographic heterogeneity of the substrate may be more relevant in inducing settlement and metamorphosis, providing the megalopae with adequate conditions for grip and protection against the environmental stress provoked by the highly dynamic hydrography of the open coast. Additionally, the stimulation of settlement and metamorphosis by conspecific cues, and the consequent delay of such events by the absence of the stimuli have been documented for gregarious species (Jensen 1989, 1991, Gebauer *et al.* 2003). However, populations of *A. hassleri* are not gregarious, displaying interference and territorial behaviours that restrict their adult population density (Navarrete & Castilla 1990, Navarrete *et al.* 2008). The integration of these responses allows us to infer that the nature (physical, chemical and/or biological) of the cues

inducing settlement and metamorphosis in decapod crustaceans depends largely on the characteristics of the habitat and demographics of the adult populations.

The cumulative frequency curves of metamorphosed individuals exhibited similar patterns of responses for treatments with substrates, but significantly different curves for the control and the water from conspecific adults treatments. On day 22 of development, intra-group variation was closer and the differences between treatments were less than on day 18 (Fig. 3). This indicates that under the culture condition of the present experiment, the megalopa of *A. hassleri* had a window of receptivity to the stimulation of metamorphosis of four days on average. If in this period, the larva could not find the adequate stimulus, a spontaneous metamorphosis occurred. This phenomenon has also been observed in other brachyuran species but with windows of receptivity of greater duration (Gebauer *et al.* 1998, 2002, 2004, 2005). Previous experiences with larval development in *A. hassleri* indicates that the optimal development of the megalopa occurs at 17°C (Barría *et al.* 2005), higher than the temperature used in this experiment (12°C). Consequently, it is expected that the megalopae near their thermic optimum accelerate their development time and thus reduce their window of receptivity. However, considering that the exposed rocky intertidal environments are structurally heterogeneous, and the metamorphosis of *A. hassleri* was mainly influenced by the physiognomy of the substrate, the probability that competent larvae will find the necessary support and shelter conditions in these environments seems to be quite high.

The survival of the megalopa was low and independent of experimental treatment. Drastic declines in the survival of this stage have been reported previously for this species and for other brachyuran crabs *e.g.*, *Cancer magister* and *N. granulata* (Sulkin & McKeen 1996, Ismael *et al.* 1997, Barría *et al.* 2005). In general, high mortality at the megalopa stage has been attributed to increased sensitivity to environmental changes, due to the metamorphosis and pelagic-benthic transition having implicit important physiological changes such as reduced metabolism, primarily by lower respiration, feeding, and growth rates (Anger 2001). However, it should be noted that in all cases, including the present study, the megalopae culture conditions maybe nutritionally deficient as *Artemia* sp. nauplii are not the best possible food. Although this has not been experimentally tested, it is possible that the culture conditions could have a significant degree of responsibility

in the mortality, acting as an experimental artefact.

From this study we concludes that: 1) the duration of the megalopa stage in *A. hassleri* is a plastic trait strongly influenced by the presence or absence of a suitable substrate; 2) certain physical properties of the substrate such as surface texture or topography may be more important in inducing settlement and metamorphosis than any chemical cue; 3) the absence of a suitable substrate is not a critical factor that affects the mortality, because the competent larvae are capable of spontaneous metamorphosis. Comparing the results of this study with previous reports on other brachyuran crabs, it is possible to postulate that there are species-specific associations between the type of stimuli that induce metamorphosis, population attributes and habitat characteristics. However, additional case studies are required in order to establish cause and effect relationships within these correlational patterns.

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