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Development and behavior of megalopa larvae and juveniles of the hydrothermal vent crab *Bythograea thermydron*

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ABSTRACT: We collected megalopa larvae and early juveniles of the crab *Bythograea thermydron* from a depth of 2500 to 2600 m at a hydrothermal vent field along the East Pacific Rise (ca 9° to 10° N, 104° W). Taxonomic identification of the megalopa larvae was accomplished through the use of morphological characteristics corroborated by molecular genetic analysis of an amplified portion of DNA from the mitochondrial 16s rRNA gene. We successfully reared megalopa larvae through metamorphosis and through subsequent juvenile molts at atmospheric pressure in the laboratory. This is the first time that this has been reported for any vent species. Laboratory data were combined with measurements of field-caught juveniles to allow estimation of carapace width, dry weight, and stage duration of the first 5 juvenile stages. Results of behavioral experiments indicated that *B. thermydron* megalopae swim actively over the range of temperature expected near the vents (2 to 25°C). Swimming speed varied with temperature (4 to 10 cm s^{-1}), but generally exceeded the speed of bottom currents at the vent fields. Moreover, the propensity to swim was inversely related to temperature. These results suggest that swimming behavior may be an important component of locating warm vent settlement sites in the otherwise cold waters surrounding a vent field.

KEY WORDS: Hydrothermal vents · Crab · Megalopa · Juvenile · Behavior · Development

INTRODUCTION

Hydrothermal vent sites are found along rift valleys that are associated with sea floor spreading in each of the major ocean basins. The spatial distribution of these areas is patchy, and active sites may be separated by hundreds of kilometers (Fornari & Embley 1995). The sites are dynamic with frequent eruptions resulting in multiple vents that spew hot water into the ambient deep sea environment. Individual vents are ephemeral and have a life expectancy on the order of decades (Haymon et al. 1993). Hot water that flows from the vents forms a plume that rises several hundred meters in the water column until it cools sufficiently to reach neutral buoyancy. At that point the plume begins to flow horizontally along the axis of the rift valley, thus providing a mechanism for chemical and biological communication among vent sites (Mullineaux et al. 1995). Water exiting the vents is rich in sulfides, and primary production by chemosynthetic bacteria supports dense assemblages of macro-invertebrates at the sites (Corliss et al. 1979). These communities are characterized by high endemism (Berg 1985) and are dominated by mollusks, vestimentiferan tube worms, and decapod crustaceans (Grassle 1986). Newly formed vents are rapidly colonized by endemic species, and the faunal composition at widely separated vent fields is quite similar (Turner et al. 1985, Tunnicliffe 1991).

This finding has led investigators to focus on questions regarding the colonization of newly formed vents and the maintenance of populations at these sites. Present evidence indicates that most vent species produce free-living larval forms that are dispersed by prevailing currents (e.g., Berg & Van Dover 1987, Wiebe et al. 1988, Kim et al. 1994, Herring & Dixon 1998). However, the essentials of this process are unclear, and the problem has been exacerbated by the difficulty of sampling in this environment, by the lack of detailed infor-

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mation on current patterns, and by the inability to identify larval forms in the field or to rear them in the laboratory. An area of recent controversy concerns the relative importance of transport via vent-driven plumes (Mullineaux & France 1995, Mullineaux et al. 1995) versus transport in the adjacent bottom currents (Kim & Mullineaux 1998).

The crab *Bythograea thermydron* is a dominant vent species that appears to have pelagic larvae. The species is a common predator at vent sites throughout the eastern Pacific. Females produce large numbers of eggs, which are brooded on the ventral surface of the abdomen in typical crab fashion (Williams 1980). While very few larvae have been collected in the field, available evidence suggests that development includes an undetermined number of zoeal stages followed by a megalopal stage (Van Dover et al. 1984, 1985). Megalopa larvae are unusual in the crab-like shape of their carapace, in their extremely large size (>8 mm carapace width), and in their bright red coloration (Williams 1980). Physiological studies have indicated that adult *B. thermydron* are tolerant of wide variation in temperature, dissolved oxygen, and hydrogen sulfide, but are incapable of long term survival outside of the high pressure environment of the deep sea (Mickel & Childress 1982a, Vetter et al. 1987, Airriess & Childress 1994). Adults are found predominantly in the warm water (>20°C) surrounding mussel and vestimentiferan beds. However, they are also found at the periphery of vent areas where temperature is about 2°C. They have been observed feeding on vestimentiferans and probably prey on vent clams, mussels, and polychaetes, as well (Mickel & Childress 1982a, Grassle 1986).

During a recent cruise to hydrothermal vent fields in the eastern Pacific, we collected megalopa larvae of *Bythograea thermydron* from a depth of 2500 to 2600 m and have successfully reared some of these larvae through metamorphosis in the laboratory at atmospheric pressure. This is the first time that this has been accomplished for any vent species. In this paper we present results of an attendant investigation of the growth, development, and behavior of the megalopa larvae and early juvenile stages of *B. thermydron*. We discuss these results in light of the dispersal of *B. thermydron* larvae among vent sites. Furthermore, we present molecular evidence corroborating the identification of these larvae as the megalopa form of *B. thermydron*.

METHODS

Collection and culture. Field work was done in November and December 1997 on the RV 'Atlantis'. Megalopa larvae and early juveniles of *Bythograea thermydron* Williams were collected from a depth of 2500 to 2600 m at a well known area of hydrothermal vent fields along the East Pacific Rise (9° to 10° N, 104° W). Vestimentiferan tube worms *Riftia pachyptila*, along with associated fauna, were collected using the manipulator arm on the submersible 'Alvin' and returned to the surface in an insulated container. Megalopae and juveniles were removed from the samples and placed individually in containers filled with 100 ml clean sea water at 34‰, 20°C. The animals were then reared at atmospheric pressure for the duration of the cruise. Because of equipment limitations onboard ship, we were unable to control light/dark cycle during this phase of the investigation. We fed the megalopae and juveniles a daily ration of newly hatched brine shrimp larvae (*Artemia* sp.) along with small pieces of tissue from the vent mussel *Bathymodiolus thermophilus*. Water in the containers was changed daily. Individuals that died onboard ship were frozen for later analysis. At termination of the cruise, surviving larvae and juveniles were transported by air to our laboratory in Lewes, Delaware, on the east coast of the USA, wherein the animals were reared under conditions similar to those above. Once in the controlled conditions of the laboratory, we reared the larvae and juveniles in constant darkness in order to more closely match conditions at the vent site. Exuvia of animals that had successfully molted were removed for determination of carapace width (CW) and length (CL).

Verification of species. We identified the megalopae and juveniles using morphological characteristics described in Williams (1980). However, 2 closely related species of brachyuran crab (*Bythograea thermydron* and *Cyanograea praedator*) occur at this vent site, and neither species has been reared from the egg to the megalopa stage. Thus, the published morphological descriptions of field-collected *B. thermydron* megalopae have not been confirmed by laboratory observations. Accordingly, we used molecular techniques to corroborate the identification of these megalopae (Olson et al. 1991). This consisted of extracting DNA from frozen specimens (–80°C) of megalopae, adult *B. thermydron*, and adult *Cyanograea praedator* using an Isoquick DNA Extraction Kit (ORCA, Inc.). A 560 base-pair portion of the mitochondrial 16s rRNA gene was amplified by the polymerase chain reaction (PCR) using the universal primers 16SAR5' (CGCCTGTTTATCAAAAACAT) and 16SBR5' (ACGTGATCTGAGTTCAGACCGG) (S. Palumbi, A. Martin, S. Romano, W. McMillan, L. Stice, G. Grabowski, University of Hawaii, USA, unpubl. data). PCR reactions were performed in 50 µl volumes where each reaction contained a final concentration of

0.1 µM for each primer, 200 µM for each deoxyribonucleoside triphosphate, 1.5 mM $MgCl_2$, 1.125 U of Taq polymerase (Promega, Madison, WI) , and 1X Promega Taq PCR buffer. Thermal cycling conditions were 1 min at 94°C, followed by 1 min at 52°C, and 2 min at 72°C. This sequence was run for 35 cycles, terminating with a 7 min final extension at 72°C. Each amplification product was subjected to restriction-length polymorphism (RFLP) analysis using the restriction endonuclease VspI (2 h at 37°C). Restriction products were visualized on a 3% agarose gel stained with ethidium bromide. As a control measure, aliquots of the amplification products were also subjected to a second RFLP analysis using the endonuclease AluI, which was known to cut PCR products of both species.

Growth and development. We measured CW and CL of all freshly collected megalopae and juveniles. We then plotted CW/CL co-ordinates for each of the more than 100 juvenile crabs collected during the cruise. These co-ordinates fell into discrete clusters that we interpreted as size intervals for the first 5 juvenile stages. We corroborated the results of this analysis by comparing these graphically determined intervals to a set of CW/CL measurements from juveniles of known stage. These consisted of 2 individuals that were collected as megalopae and 9 individuals that were collected as stage 1 juveniles. Both of the megalopae metamorphosed and survived to the 3rd stage in the laboratory, while all 9 of the juveniles survived to the 3rd stage, 3 to the 4th stage, and 1 to the 5th stage. Because crab size is most commonly expressed in terms of carapace width, we used the results of the above graphical analysis to calculate mean CW for each of the stages. In addition, we used results of the rearing study to determine duration of each of the first 4 larval stages under laboratory conditions. Finally, we determined dry weight (48 h, 60°C, analytical balance) for 4 haphazardly chosen juveniles from each size class and used these data to calculate a representative dry weight for each of the juvenile stages.

Swimming and walking behavior. We measured swimming and walking speeds of individual megalopae at 6 different temperatures ranging from 2 to 25°C (n = 10 megalopae per temperature). Larvae used in the experiments were cultured at 20°C and were acclimated to experimental temperatures in steps of 5°C. The duration of each step was 24 h. Because of the limited number of larvae available, the same 10 individuals were tested at each of the 6 temperatures (see below for statistical approach). Each combination of an individual larva and a particular temperature was termed an 'experimental trial' Experiments were run in a chamber (60 cm long × 15 cm wide × 25 cm deep) constructed of clear plastic and filled with 18 l of filtered sea water of the appropriate temperature. The bottom was marked with a 1 cm × 1 cm grid, and the outside of the tank was insulated to minimize temperature change over the course of an experiment. Normal room light was provided by overhead cool-white fluorescent lamps (8.0×10^{13} quanta cm^{-2} s^{-1} at the surface of the water), and movement of the larvae was recorded by a video camera system for periods up to 5 min.

We determined the speeds of swimming and walking by conducting a frame analysis of each experimental trial. This consisted of advancing the videotape frame-by-frame and using the bottom grid to determine the distance that a larva had moved per frame. Because we knew the number of frames recorded per second (60), we could use this information to calculate the speed at which the megalopae were moving. Analysis of each experimental trial consisted of 3 determinations of walking speed and 3 determinations of swimming speed, with each determination made over a distance of at least 5 cm. We took care to analyze only those segments of tape wherein megalopae were engaged in sustained swimming or walking. Subsequent evaluation was always conducted using the fastest of the 3 determinations for each of the 10 replicate megalopae. Effects of temperature on swimming speed and on walking speed were assessed using analysis of variance for repeated measures (Sokal 1995). This type of analysis takes into consideration the repeated use of the same larvae at each of the experimental temperatures. In this case, the analysis considers temperature a fixed factor and individual megalopae as a random factor. Calculations are done as a 2-way ANOVA without replication.

Because we were concerned that room light might affect larval behavior, we also conducted a set of preliminary trials at 20°C in a light-tight room illuminated by ordinary incandescent light passed through Kodak red filters (<0.1% transmission at wavelengths below 600 nm). We chose this wavelength because previous studies had shown that crab larvae generally do not respond to light at wave lengths >600 nm (Cronin & Forward 1988). Furthermore, we had access to unpublished data indicating that the visual pigments of *Bythograea thermydron* megalopae are especially adapted to short wavelengths (480 nm) with little ability to absorb far red light (T. Cronin, University of Maryland, Baltimore County, USA). Results of repeated-measures ANOVA showed no significant difference in mean swimming speed of megalopae under room light or red light ($\alpha = 0.05$; df = 1,9; $p = 0.155$). In addition there was no effect of individual megalopae ($\alpha = 0.05$; df = 9,9; $p = 0.101$).

In another set of experiments, we determined the effect of temperature on the duration of swimming in still water. Individual larvae were introduced to the

experimental chamber (see above) and allowed to swim to the surface. Duration of uninterrupted swimming was determined for a maximum of 5 min using a timer feature on the video system. Larvae were always temperature-acclimated (see above) before use in a trial, and a single determination of swimming duration was made during each trial (n = 10 megalopae per temperature). Because of the limited number of individuals available, the same individuals were used in each of the 6 trials. Thus, effects of temperature on swimming duration were assessed by repeated-measures ANOVA.

These experiments were run under normal room light. However, we also ran a preliminary set of trials under far red light at 20°C (see above). Results of repeated-measures ANOVA showed no significant difference in mean duration of swimming under room light or red light ($\alpha = 0.05$; df = 1, 9; $p = 0.184$). Moreover, there was no significant effect of individual megalopae on duration ($\alpha = 0.05$; df = 9, 9; $p = 0.388$).

In addition to the above experiments in still water, we ran a set of trials at 20°C in a 2 m long flume (cross sectional area = 23 cm^2) that allowed a range of flow from still water to 8 cm s^{-1}. Larvae were introduced to the mid-point of the flume, and their motion was recorded until they reached either end of the apparatus. The bottom of the flume was marked with a grid that allowed frame analysis similar to that used in the still-water experiments.

RESULTS

Identification, growth, and development

A total of 73 megalopae and 122 juveniles were collected alive during the cruise. Morphological characteristics of the megalopae and juveniles matched those in the original description of *Bythograea thermydron* (Williams 1980). RFLP analysis demonstrated that mitochondrial DNA from the megalopa larvae and from adult *B. thermydron* contained 1 diagnostic restriction site for VspI, resulting in 2 distinct bands, while products from the co-occurring crab *Cyanograea praedator* lacked any sites (Fig. 1). The enzyme AluI restricted mitochondrial DNA from both species, which assured that DNA from *C. praedator* was not generally refractory to RFLP analysis.

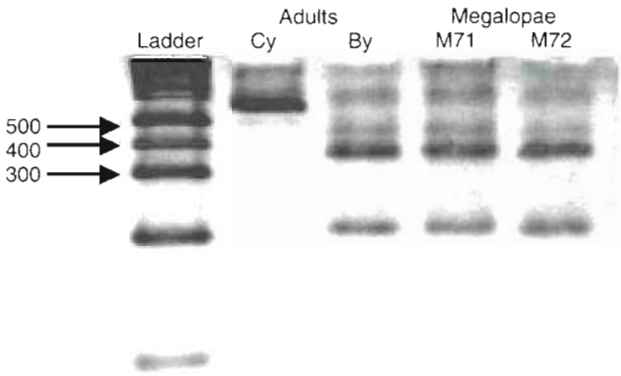

Fig. 1. *Bythograea thermydron*. Molecular confirmation of megalopa larvae by RFLP analysis. Cy = adult *Cyanograea praedator*. By = adult *B. thermydron*. M71 = megalopa specimen 1. M72 = megalopa specimen 2. Ladder refers to a known molecular weight marker used to estimate fragment size

Six megalopae molted successfully to the juvenile stage, and 2 of these individuals survived through at least 1 more molt in the laboratory. However, larvae that failed to molt within 18 d of collection remained in the megalopa stage indefinitely. Some of these individuals were held in the laboratory in an otherwise healthy condition for the duration of the investigation (201 d). Fourteen field-collected juveniles underwent at least 1 molt in the laboratory. Nine of these crabs initiated a second molt and 1 individual survived through a total of 3 molts. Duration of the first juvenile stage was around 15 d under laboratory conditions and increased considerably in subsequent stages, but with

Table 1. *Bythograea thermydron*. Carapace width, dry weight, and stage duration of early life history stages. Values are mean ± 95% confidence interval. Dry weights were determined for 4 representative crabs from each developmental stage. Crabs were reared in the laboratory at 20°C. Dashes indicate no data

	Developmental stage					
	Meg.	J-1	J-2	J-3	J-4	J-5
Width (mm)	7.9 ± 0.3 N = 73	9.3 ± 0.3 N = 42	11.3 ± 0.4 N = 51	13.2 ± 0.6 N = 26	14.6 ± 0.2 N = 12	16.7 ± 0.4 N = 8
Weight (mg)	37.7 ± 1.7 N = 4	49.4 ± 5.1 N = 4	72.3 ± 13.5 N = 4	127.8 ± 12.6 N = 4	186.3 ± 29.3 N = 4	269.5 ± 18.7 N = 4
Duration (d)	–	14.5 N = 2	31.3 ± 8.9 N = 11	41.3 ± 10.4 N = 6	33.0 N = 1	–

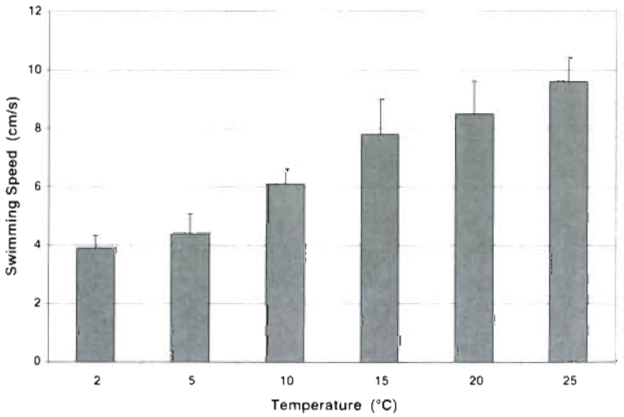

Fig. 2. *Bythograea thermydron*. Effect of temperature on swimming speed of megalopa larvae. Values are mean ± 95% confidence interval. N = 10 megalopae per temperature

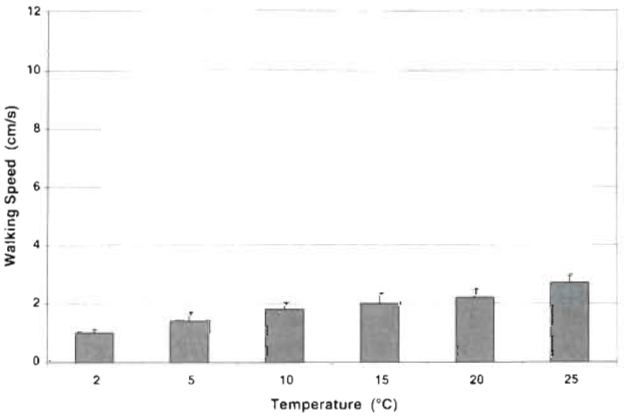

Fig. 3. *Bythograea thermydron*. Effect of temperature on walking speed of megalopa larvae. Values are mean ± 95% confidence interval. N = 10 megalopae per temperature

substantial variation among individual crabs (Table 1). Mortality of juvenile crabs was almost always associated with molting, and maximum survival in the laboratory was 199 d. Analysis of CW/CL co-ordinates indicated that juvenile crabs increased in CW from approximately 8 mm at Stage 1 to around 22 mm by Stage 5. Dry weight increased from about 40 mg in the 1st juvenile stage to nearly 270 mg by the 5th stage.

Swimming and walking behavior

Megalopae used in these experiments were apparently healthy individuals that had failed to molt within 18 d of collection. Analysis of variance for repeated measures showed a significant effect of temperature on both mean swimming speed ($\alpha = 0.05$; df = 5, 45; $p < 0.001$) and mean walking speed ($\alpha = 0.05$; df = 5, 45; $p < 0.001$). There was no significant effect of individual megalopae on walking speed ($\alpha = 0.05$; df = 9, 45; $p = 0.055$). However, there was a significant effect on swimming speed ($\alpha = 0.05$; df = 9, 45; $p = 0.004$). While this indicates that the response to temperature was not uniform across individual megalopae, it does not affect the general inference of a strong effect of temperature on mean swimming speed (Sokal 1995).

Overall, the mean swimming speed in still water ranged from approximately 4 to 10 cm s^{-1} (Fig. 2), and walking speed varied from approximately 1 to 3 cm s^{-1} (Fig. 3). When placed in moving water in the flume at 20°C, larvae showed no consistent orientation to flow, but were easily able to swim upstream at maximum flow rates (ca 8 cm s^{-1}).

Mean duration of uninterrupted swimming in still water ranged from approximately 5 s at high temperature to nearly 175 s at low temperature (Fig. 4). Analysis of variance for repeated measures showed a significant effect of temperature ($\alpha = 0.05$; df = 5, 45; $p < 0.001$), but no effect of individual megalopae ($\alpha = 0.05$; df = 9, 45; $p = 0.132$).

DISCUSSION

The use of traditional morphological analysis combined with results of our molecular technique provide strong evidence that megalopa larvae used in this study belong to the species *Bythograea thermydron*. The VspI restriction pattern from the segments of mitochondrial 16s rRNA gene that we isolated from the megalopal specimens were clearly identical to that from adult *B. thermydron* and were unequivocally different from the pattern in *Cyanograea praedator*. Moreover, the enzyme AluI restricted PCR products from both species, which assured that the DNA that we

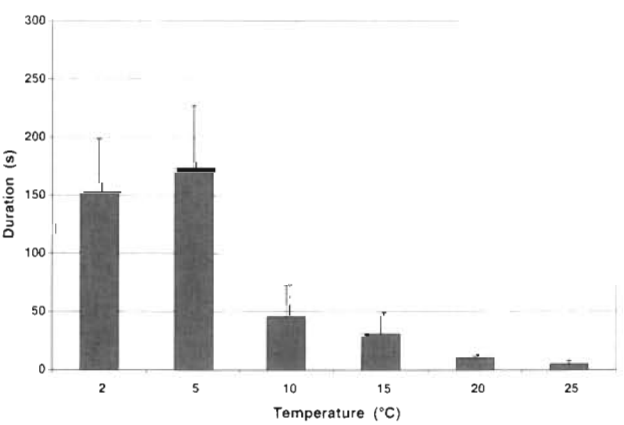

Fig. 4. *Bythograea thermydron*. Effect of temperature on the duration of uninterrupted swimming by megalopa larvae. Values are mean ± 95% confidence interval. N = 10 megalopae per temperature

obtained from *C. praedator* was not generally refractory to RFLP analysis. Nevertheless, the fact that VspI failed to restrict *C. praedator* at all, allows some small degree of ambiguity in our results, i.e. we could not totally exclude the possibility of a technical artifact in the *C. praedator* restriction. However, all of the megalopae collected in our study had gross morphological features that matched published descriptions for *B. thermydron*, and several of these megalopae molted to the juvenile stage in the laboratory. Because the juvenile stages of *B. thermydron* are reliably identified from published descriptions of gross morphology, there can be little doubt that the megalopae used in our study belong to this species (Williams 1980).

With the taxonomic issues settled, our study has shown that megalopa larvae and early juveniles of this species are capable of growth and development at pressures ranging from ambient-surface to at least 260 atmospheres (≈26 MPa). This is in contrast to the adult form of *Bythograea thermydron*, which suffers cardiac dysfunction, loss of motor coordination, and eventual death upon decompression to surface conditions (Mickel & Childress 1982a). Effects of depressurization on adult *B. thermydron* are related to changes in cell membranes and are ultimately attributable to changes in the homeoviscous properties of lipids that are integral to the structure of these membranes (Airriess & Childress 1994) In *B. thermydron* this effect is ameliorated by low temperature, and adult crabs held at 5°C show no effect on cardiac performance at pressures ranging from approximately 7 to 40 MPa (Mickel & Childress 1982a, Airriess & Childress 1994). Thus, while adult *B. thermydron* are incapable of existence at depths above 700 m (and have never been collected at depths above 2500 m), they nonetheless show a remarkable range of tolerance for variation in pressure. The physiological mechanisms that allow the even further extension of this range by megalopa larvae and early juveniles are unknown, but this extremely wide tolerance provides the potential for a great deal of flexibility in the vertical position of the megalopa larvae in the water column.

Juveniles survived for periods as long as 199 d in the laboratory at atmospheric pressure and underwent as many as 3 consecutive molts. Temperature in the laboratory cultures (20°C) was similar to that in the vestimentiferan clumps wherein the juveniles were collected. Available field data (corroborated by discrete laboratory measurements) allowed reasonable estimates of mean size (carapace width and dry weight) for the megalopa stage and for 5 juvenile stages. Laboratory data also allowed estimation of mean duration of 4 juvenile stages. However, these estimates of stage duration were insufficient for use in determination of growth rates because of the small number of individuals involved in the laboratory study and the high variation in stage duration among those individuals. We have instead presented mean carapace width and dry weight for megalopa larvae and for the respective juvenile stages. This allows determination of the stage of development of field collected juveniles, but it does not allow estimation of the age of these individuals. Only 2 other studies have dealt with growth of deep sea crabs. In a laboratory study, Van Heukelem et al. (1983) reared larvae of the bathyal crab *Chaceon* (*Geryon*) *quinquedens* at 12°C and determined that CW growth was linear at a mean rate of 0.06 mm d^{-1}. The authors calculated that *C. quinquedens* would reach maturity in approximately 5 yr at this growth rate. In a different approach, Bennett & Turekian (1984) conducted a radiometric analysis of uranium and thorium decay chains in minerals found in the carapace of *Bythograea thermydron* under actual field conditions and concluded that intermolt duration for large adult crabs may be as long as 3 to 4 yr. If correct, this indicates that *B. thermydron* has a long life span, but says little about growth rates of the juvenile stages.

Mortality among juvenile *Bythograea thermydron* was almost always associated with molting, which has also been reported for the juvenile forms of shallow water crabs under laboratory conditions (Dittel & Epifanio 1984, Epifanio et al. 1998). Otherwise, the juvenile crabs in our investigation appeared vigorous and healthy. They displayed normal motor coordination, consumed their full ration, and showed typical crab behaviors. Thus, it is unclear why no crabs survived beyond the 5th juvenile stage in the laboratory. It is tempting to speculate that the older juveniles in our study had begun to undergo ontogenetic changes concerning their sensitivity to low pressure, but we have no physiological evidence to support this idea.

As with the juveniles, mortality among the megalopa larvae was usually associated with molting. Successful molts always occurred within 18 d of collection. The remaining megalopae were active and apparently healthy throughout the course of the investigation. Thus, it is not clear why these larvae failed to undergo metamorphosis to the 1st juvenile stage. Studies of the metamorphosis of shallow water crabs have demonstrated the role of inductive chemical cues associated with adult habitat, but megalopae in these investigations eventually molted to the juvenile form, even in the absence of a cue (Forward et al. 1994, 1996). Because the megalopae collected in this investigation had already settled in adult habitat, it would seem reasonable that they were physiologically competent to undergo metamorphosis (e.g. Weber & Epifanio 1996), but the possibility still remains that megalopal development requires several months and that the larvae that metamorphosed in the laboratory were simply

older at the time of collection than those that did not metamorphose.

Megalopa larvae were tolerant of a wide range of temperature, even with minimal acclimation. This tolerance is obviously adaptive for organisms living at vent sites and has been well documented in adult *Bythograea thermydron* and other vent species (Mickel & Childress 1982b, Dahlhoff et al. 1991). Megalopae showed active swimming behavior over the entire range of temperatures (2 to 25°C) that are likely to be encountered in their natural habitat. Effects of temperature on swimming rate were muted, with a Q_{10} of 1.5 over the entire 23°C range of the experiments, compared to expected values of 2 to 3 over the tolerance range of a typical shallow water crab (Prosser 1973). This suggests a highly evolved adaptation to larval dispersal in the cold water external to the vents, followed by settlement in the warm water at the vent sites.

Megalopa larvae also demonstrated active walking behavior over the range of temperatures in our experiments, and again the effect of temperature was muted with a Q_{10} of 1.5. This behavior was unusual in that megalopa larvae generally walked laterally like adult crabs, rather than in an anterior/posterior direction like the megalopae of shallow water crabs. Moreover, walking was the dominant form of locomotion at temperatures above 15°C, which is again unusual in comparison to the megalopae of shallow water species (Luckenbach & Orth 1992). This may be a special adaptation for vent existence in that megalopae would swim when in the cold waters of the surrounding water column, thus augmenting dispersal. However, once encountering the warm water at a vent, the larvae would settle and explore the vent community by walking before undergoing metamorphosis.

Taken as a whole, the results of our study suggest that larval development in *Bythograea thermydron* occurs in the water column external to the vents. Our data show that the megalopa stage is physiologically capable of exploiting the entire water column from the cold bottom water surrounding the vent sites to the tropical surface waters above. However, the actual vertical distribution of the larval forms is unknown outside of a few collections of zoea and megalopa larvae from vent plumes or from open water near a vent site (Van Dover et al. 1984, L. Mullineaux, Woods Hole Oceanographic Institution, USA, unpubl. data). Nevertheless, and in contrast to preliminary speculation based on preserved specimens (Williams 1980), the megalopa stage of *B. thermydron* is an extremely good swimmer with speeds in warm water that are comparable to the fastest swimming megalopae of shallow water forms (Luckenbach & Orth 1992). Even at the temperatures typical of bottom water near the vents (2 to 5°C), the megalopa larvae are capable of sustained swimming at 4 cm s^{-1}, which is similar to the speed of tidal currents at this vent site and more than twice as great as the reported speed of subtidal bottom currents (Kim & Mullineaux 1998). Moreover, the propensity to swim increases significantly with decreasing temperature, so megalopae are likely to spend the majority of time swimming, as opposed to sitting on the bottom, when in the cold waters away from a vent site. Thus, if megalopae were to swim in the direction of a prevailing bottom current, their effective speed over bottom could be as great as 7 km d^{-1} at ambient bottom temperatures, and even in still water their speed would be around 3.5 km d^{-1}

At this point we know nothing about zoeal development, e.g., duration, swimming behavior, etc. However, zoeal swimming in shallow water forms is only important in vertical migration, and horizontal transport is largely controlled by currents. Thus, long distance dispersal of *Bythograea thermydron* may be effected by passive transport in bottom currents or in the plume, while actual selection of settlement sites may be dependent on active swimming by megalopae. If we take the results of our laboratory data literally, megalopa larvae may be able to delay metamorphosis for several months until suitable settlement habitat is encountered. So, even if swimming in the natural environment were discontinuous (e.g. 8 to 12 h d^{-1}) , the larvae of *B. thermydron* could easily swim tens to even hundreds of km in search of suitable vent sites during a megalopa stage that lasted 2 to 3 mo. The cues involved in fine-scale location of a vent or in induction of metamorphosis are unknown, but actual settlement at a site may be augmented by the inhibitory effect of high temperature on swimming.

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