Vol. 170: 231–238, 1998 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published September 3

# Early life history of *Hemigrapsus sanguineus*, a non-indigenous crab in the Middle Atlantic Bight (USA)

**C. E. Epifanio*, A. I. Dittel, S. Park, S. Schwalm, A. Fouts**

Graduate College of Marine Studies, University of Delaware, Lewes, Delaware 19958, USA

ABSTRACT: The Japanese shore crab *Hemigrapsus sanguineus* (de Haan) was recently introduced to the northeast coast of the USA. The crab has established intertidal populations extending throughout the Middle Atlantic Bight. This study defines early-life-history characteristics that are germane to range extension in this species. Results of the investigation showed that the spawning season of *H. sanguineus* continues for at least 4 mo in the southern Middle Atlantic Bight. This is considerably longer than the spawning seasons of co-occurring native crabs. Eggs hatch about 14 d after extrusion, and females have the potential to produce several broods each year. Zoeal larvae are tolerant of a wide range of temperature/salinity combinations, and mean duration of zoeal development ranges from approximately 16 d at 25°C to 55 d at 15°C. At 25°C zoeae are capable of development to the megalopa stage at salinities as low as 15‰. At lower temperatures the zoeae require salinities above 20‰. The megalopa stage appears to have more stringent temperature/salinity requirements, which may restrict *H. sanguineus* to rocky shores of the coastal ocean and the adjacent high-salinity regions of the estuary. Under these conditions megalopae molt to the first juvenile stage in approximately 25 d post hatching. Newly metamorphosed crabs reach the fifth juvenile instar in 35 d. Dry-weight growth of zoeal larvae and early stage juveniles is exponential at respective rates of 23 and 8% of body weight per day.

KEY WORDS: Non-indigenous · Exotic · Crab · Larvae · Juvenile · Growth

## INTRODUCTION

There has been a great deal of study of the occurrence of non-indigenous (exotic) species in terrestrial ecosystems where introductions have often caused large changes in native biota (for reviews see Kornberg & Williamson 1986, Mooney & Drake 1986, Lodge 1993). Effects of non-indigenous species in fresh-water systems have also been severe, as evidenced by the recent spread of the zebra mussel *Dreissena polymorpha* and the Asiatic clam *Corbicula fluminea* in the river systems of North America and Europe (e.g. Araujo et al. 1993, French & Schloesser 1996, Johnson & Carlton 1996). Marine environments differ from terrestrial and fresh-water systems in that much of the biota exhibits a complex life cycle including free-living planktonic forms that can be transported by currents over long distances. Consequently, marine species are often distributed over a wide latitudinal range, and assemblages living in any particular area of the range may be part of one interbreeding population that extends for hundreds of kilometers. Nevertheless, there are many barriers that restrict the natural range of marine species. These include latitudinal variation in temperature, as well as the existence of continental land masses and wide ocean basins. Marine ecosystems that occur on either side of a natural barrier may have distinctly different evolutionary histories, and the introduction of exotic species can have effects that are as pronounced as those seen in terrestrial and fresh-water systems (Johnson 1994).

Interest in marine and estuarine environments has focused both on the introduction of exotic species associated with maricultural activities (e.g. Wingate et al. 1991, Barber & Mann 1994, Everett et al. 1995) and on

*E-mail: epi@udel.edu

the escape of non-indigenous forms via release of ballast water from ocean-going ships (e.g. Carlton et al. 1990, Hallegraeff & Bolch 1991, 1992, Cohen & Carlton 1997). A recent study of Asian ships arriving at a port in Oregon (USA) illustrates the magnitude of the problem. Carlton & Geller (1993) surveyed ballast water from approximately 150 ships and found more than 350 taxa representing 16 animal phyla, 3 protist phyla, and 3 plant divisions. Meroplanktonic forms were very abundant, with densities of invertebrate larvae often greater than 200 $m^{-3}$. While the fate of these larvae in Oregon waters has not been determined, established populations of ballast-transported exotics have been well documented in areas as diverse as San Francisco Bay (Carlton et al. 1990), the Black Sea (Shuskina & Musayeva 1990), and the temperate east coast of Australia (Williams et al. 1988).

There have been no systematic studies of ballast-water introductions on the Atlantic coast of North America; however, a number of probable cases have been identified (e.g. Brenchley & Carlton 1983, Allmon & Sebens 1988, Berman et al. 1992, Lambert et al. 1992). Among these is the brachyuran crab *Hemigrapsus sanguineus* (de Haan) (family: Grapsidae). This species is native to the western Pacific and is common in rocky intertidal habitats throughout Japan, Korea, and temperate China (Sakai 1976, Ai-yun & Yang 1991). An exotic population of this species was first identified in 1988 near Cape May at the mouth of Delaware Bay, USA (ca 39° N, 75° W), and the species has now become established from Pamlico Sound, North Carolina, to Cape Cod, Massachusetts (Williams & McDermott 1990, McDermott 1991, Lafferty & Kuris 1996). While it is not clear that this rapid proliferation has resulted from a single introduction, the biological parameters that will control ultimate range extension are poorly known, and in particular there is little information about critical early-life-history characteristics of the species.

Mature *Hemigrapsus sanguineus* range from 15 to 50 mm in carapace width (Fukui 1988). Five zoeal stages and a megalopal stage have been described, but larval duration has not been determined for the seasonal range of salinity and temperature in the native habitat of the species (Kurata 1968, Hwang & Kim 1995). Adults in native areas are restricted to the middle and upper zones of the rocky intertidal (Fukui 1988). However, an exotic population of *H. sanguineus* in Long Island Sound (USA) has been found to range throughout the entire intertidal, with abundance exceeding that of co-occurring native crabs and often reaching 30 $m^{-2}$ (Lohrer & Whitlatch 1997). Adults consume a variety of food types (macroalgae, barnacles, small crustaceans, snails, bivalve mollusks, polychaetes), which in Long Island Sound overlap with food preferences of sympatric native species of crab. Habitat preference, prey types, and growth rates of early juveniles are not known, and there is no information on larval biology beyond anatomical descriptions of the stages (Terada 1974, 1981, Gamo & Muraoka 1977).

In this paper we present results of a study of the effects of varying environmental conditions on growth and development of larvae and early juveniles of *Hemigrapsus sanguineus*, paying particular attention to factors that may affect range extension. These include (1) effects of temperature and salinity on development, growth, and survival of the larval stages, (2) growth rates of early juveniles, and (3) duration of the spawning season in the Middle Atlantic Bight.

## METHODS

**Culture techniques.** Gravid females were collected from a rocky intertidal area near Cape Henlopen at the southern terminus of Delaware Bay and held in filtered sea water (25°C, 30‰) until hatching. We reared larvae under static conditions with a diet of newly hatched nauplii of brine shrimp (*Artemia* sp.) at a density of 5000 nauplii $l^{-1}$. Rations were always replenished on a daily basis. We used larvae from 3 to 4 broods in each experiment. All sea water used in the experiments was filtered to remove particles >5 µm, and salinity was adjusted by dilution with de-ionized water. All experiments were conducted in environmental chambers in which temperature (±0.5°C) and photoperiod (14 h light:10 h dark) were controlled.

Newly hatched larvae from the various broods were mixed haphazardly before assignment to the different treatments. In experiments that measured survival, larvae were reared in 50 ml of filtered sea water in small glass bowls (7.5 cm diameter) at 10 larvae per bowl. Larvae were transferred to clean sea water daily, at which time survivorship and molt frequency were determined. In experiments that measured growth rate, larvae were reared in 1000 ml of filtered sea water in large glass bowls (19 cm diameter) at 200 per bowl and transferred to clean sea water every 48 h. We reared newly metamorphosed juveniles individually in compartmentalized plastic boxes (50 ml sea water per compartment) in order to determine molt frequency and rates of growth.

**Effects of temperature and salinity.** We assessed zoeal duration and survival at 15 combinations of salinity (10, 15, 20, 25, 30‰) and temperature (15, 20, 25°C). In Expt 1, we investigated effects of the 3 higher salinities when combined with each of the 3 temperatures. We extended the investigation in Expt 2 to compare effects of the 2 lower salinities. Expt 1 was a 3 × 3 fac-

torial, and Expt 2 was a 2 × 3 factorial. These experiments were analyzed in separate statistical exercises. For every treatment, percentage survival from hatching to the megalopa stage was determined for each of 6 replicate bowls, and mean values (arcsin transformed) were compared by 2-way ANOVA ($\alpha = 0.05$). At initiation of the experiments, replicate bowls in the various treatments contained 10 larvae each. For every bowl we determined the number of days from hatching to the megalopa stage for each surviving larva and calculated the average time to megalopa (ATM) for the larvae in each bowl. For each treatment we calculated the mean of the 6 replicate ATM. These values, which represented the duration of zoeal development in each treatment, were compared by 2-way ANOVA (as above). The design of the megalopal experiments was identical, but due to the small number of treatments in which megalopae survived to crab stage 1, we did not subject those data to ANOVA.

Another group of larvae was reared at each of the 15 combinations of salinity and temperature in order to determine rates of growth. We measured changes in dry weight in each treatment every 48 h throughout zoeal development. This was done by removing 6 larvae from each treatment, rinsing them in de-ionized water, drying them at 60°C for 48 h, and weighing individuals on a Mettler microbalance (accuracy = 0.1 µg). For each treatment we fit the time series of dry-weight data to an exponential model ($W_t = W_0 e^{gt}$), where $W$ is dry weight (µg), $t$ is time (days), and $g$ is the specific growth rate ($d^{-1}$).

**Growth and development of juvenile crabs.** In order to determine the maximum growth rate of early juveniles, 10 individuals were held at 25°C/30‰ starting on the morning after they molted from the megalopa stage to crab stage 1. We chose this salinity/temperature combination because it had resulted in high survival and rapid growth of zoea and megalopa larvae (see 'Results'). Crabs were fed a daily ration of newly hatched brine shrimp and were transferred to clean water every 48 h. Each crab was observed daily for molting, and exuvia were measured for later determination of carapace growth rates. We reared another group of newly metamorphosed juveniles under similar conditions to determine the rate of dry-weight growth. A sub-sample of crabs was removed from the population every 5 d for determination of dry weight and calculation of growth coefficient (see above). The experiment was terminated after 35 d.

**Seasonality of spawning.** We conducted a weekly survey (June 4 to October 23) of the proportion of gravid females in a rocky intertidal area near Cape Henlopen. This 5 mo sampling period was designed to bracket the spawning seasons of native crabs that co-occur with *Hemigrapsus sanguineus* in the local rocky intertidal environment. We sampled the same general area each week. Protocol consisted of turning over rocks and collecting individuals by hand. We made no attempt to quantify the density of crabs in the area. Sample size varied with availability (weekly mean = 16 ± 3.3 mature females). Carapace width was measured and the color of the egg mass was noted as an indicator of the age of the eggs. A sub-sample of gravid females was returned to the laboratory each week for determination of the time course of egg development. For each week we quantified the intensity of spawning as the percentage of mature females that were gravid and the percentage that were carrying early-stage eggs. At the end of the 5 mo sampling period we calculated the mean percentage of gravid and early-stage females collected during each month and during spring or neap tidal periods (as determined from predicted tidal range). Mean values were compared by 1-way ANOVA and 1-tailed $t$-test, respectively ($\alpha = 0.05$).

## RESULTS

### Effects of temperature and salinity

While the main effect of salinity on survival was not significant in Expt 1, there was a strong effect of temperature on both survival and duration of larval development (ATM) and a significant interactive effect on survival. There was a significant effect of salinity and temperature on survival and duration in Expt 2, and there was a significant interactive effect on survival (Table 1). Survival to the megalopa stage reached 60% under favorable conditions and was generally highest

Table 1. *Hemigrapsus sanguineus*. Effects of temperature and salinity on zoeal survival and duration of development to the megalopa stage. Summary of ANOVA. T: temperature; S: salinity; p: probability of rejecting a correct null hypothesis; nd: interactive effect could not be determined because of unbalanced design. Expt 1: T = 15, 20, 25°C; S = 20, 25, 30‰. Expt 2: T = 15, 20, 25°C; S = 10, 15‰

| | Dep. variable | Treatment | p |
|---|---|---|---|
| Expt 1 | Survival | T | $p < 0.01$ |
| | | S | $p > 0.05$ |
| | | T × S | $p < 0.01$ |
| | Duration | T | $p < 0.01$ |
| | | S | $p < 0.01$ |
| | | T × S | nd |
| Expt 2 | Survival | T | $p < 0.01$ |
| | | S | $p < 0.01$ |
| | | T × S | $p < 0.01$ |
| | Duration | T | $p < 0.01$ |
| | | S | $p < 0.01$ |
| | | T × S | nd |

Table 2. *Hemigrapsus sanguineus*. Mean percentage survival (± SD) from hatching to the megalopa stage at different combinations of temperature and salinity. n = 6 bowls of 10 larvae each in each treatment at initiation of the experiment

| Salinity (‰) | Temperature 15°C | 20°C | 25°C |
|---|---|---|---|
| 10 | 0.0 | 0.0 | 0.0 |
| 15 | 0.0 | 0.0 | 8.3 ± 9.8 |
| 20 | 0.0 | 23.3 ± 7.4 | 60.0 ± 6.3 |
| 25 | 3.3 ± 5.2 | 60.0 ± 15.3 | 50.0 ± 15.3 |
| 30 | 5.0 ± 5.5 | 60.0 ± 2.0 | 46.7 ± 16.0 |

Table 3. *Hemigrapsus sanguineus*. Mean duration (± SD) in days from hatching to the megalopa stage at different combinations of temperature and salinity. n = 6 bowls of 10 larvae each in each treatment at initiation of the experiment. Zero values indicate that no larvae survived to the megalopa stage

| Salinity (‰) | Temperature 15°C | 20°C | 25°C |
|---|---|---|---|
| 10 | 0.0 | 0.0 | 0.0 |
| 15 | 0.0 | 0.0 | 21.8 ± 1.6 |
| 20 | 0.0 | 22.8 ± 1.1 | 16.4 ± 0.1 |
| 25 | 54.5 ± 1.5 | 21.5 ± 0.3 | 15.9 ± 0.4 |
| 30 | 53.0 ± 0.8 | 20.8 ± 0.3 | 15.6 ± 0.3 |

Table 4. *Hemigrapsus sanguineus*. Mean percentage survival (± SD) from hatching to crab stage 1 at different combinations of temperature and salinity

| Salinity (‰) | Temperature 15°C | 20°C | 25°C |
|---|---|---|---|
| 10 | 0.0 | 0.0 | 0.0 |
| 15 | 0.0 | 0.0 | 0.0 |
| 20 | 0.0 | 0.0 | 0.0 |
| 25 | 0.0 | 0.0 | 1.7 ± 3.7 |
| 30 | 0.0 | 3.3 ± 5.2 | 16.7 ± 15.1 |

Table 5. *Hemigrapsus sanguineus*. Mean duration (± SD) in days from hatching to crab stage 1 at different combinations of temperature and salinity. Zero values indicate that no larvae survived to crab stage

| Salinity (‰) | Temperature 15°C | 20°C | 25°C |
|---|---|---|---|
| 10 | 0.0 | 0.0 | 0.0 |
| 15 | 0.0 | 0.0 | 0.0 |
| 20 | 0.0 | 0.0 | 0.0 |
| 25 | 0.0 | 0.0 | 29.0 |
| 30 | 0.0 | 37.5 ± 6.4 | 25.4 ± 3.1 |

Table 6. *Hemigrapsus sanguineus*. Growth in dry weight from hatching to the megalopa stage at different combinations of temperature and salinity. Values are specific growth rates ($d^{-1}$). Zero values indicate no larvae survived to megalopa stage. n = 6 bowls of 10 larvae each in each treatment

| Salinity (‰) | Temperature 15°C | 20°C | 25°C |
|---|---|---|---|
| 10 | 0.0 | 0.0 | 0.0 |
| 15 | 0.0 | 0.0 | 0.12 |
| 20 | 0.0 | 0.12 | 0.23 |
| 25 | 0.08 | 0.13 | 0.19 |
| 30 | 0.07 | 0.13 | 0.21 |

at temperatures above 15°C and salinities above 15‰ (Table 2). No larvae survived beyond zoeal stage 2 at a salinity of 10‰, regardless of temperature. Mean duration of the zoeal stages ranged from 16 to 55 d, depending on experimental conditions (Table 3). Larvae reared at 15°C failed to develop to the megalopa stage at salinities <25‰, while at higher temperatures larvae completed development to the megalopa stage at salinities as low as 15‰. Mortality was generally higher during the megalopa stage, and no larvae survived to crab stage 1 at 15°C or at salinities below 25‰. At 25°C/30‰, it took a mean of 25.4 d from hatching to crab stage 1, and mean survival was 16.7% (Tables 4 & 5).

Dry-weight growth of zoeal larvae was adequately described by an exponential model ($r^2$ = 0.76–0.91). Specific growth rates varied greatly with environmental conditions and ranged from 0.07 to 0.23 $d^{-1}$ (Table 6). (These respective values are roughly equivalent to dry-weight increases of 7 and 23% $d^{-1}$.) Newly hatched zoeal larvae had a mean dry weight of 11.4 µg. Under optimum conditions zoeal larvae reached maximum dry weights as great as 210 µg before molting to the megalopa stage. In turn, the dry weights of megalopae reached values as high as 475 µg shortly before metamorphosis to crab stage 1.

### Growth of early juveniles

Mean duration of the first juvenile crab stage was approximately 5 d at 25°C/30‰ (Table 7). Intermolt duration increased with succeeding molt stages, and by the end of the 35 d experiment, all juveniles had reached crab stage 5. Newly metamorphosed juveniles had a mean carapace width of 1.6 mm. Growth in carapace width was linear (rate = 0.06 mm $d^{-1}$; $r^2$ = 0.89), while growth in dry weight fit an exponential model (rate = 0.06 $d^{-1}$; $r^2$ = 0.94). On the day after molting from the megalopa stage, the mean dry weight of juve-

Table 7. *Hemigrapsus sanguineus*. Development of early juveniles. Mean day of molting was calculated as the number of days transpiring after an individual molted from the megalopa stage to crab stage 1. Mean intermolt duration was calculated in days. Mean carapace width is in mm. n = 10 for each stage

| Molt stage | Mean day molt | Intermolt duration | Carapace width |
|---|---|---|---|
| Crab stage 1 | 5.1 ± 1.2 | 5.1 ± 2.1 | 1.6 ± 0.1 |
| Crab stage 2 | 11.0 ± 1.4 | 5.9 ± 0.7 | 1.9 ± 0.1 |
| Crab stage 3 | 18.1 ± 2.0 | 7.1 ± 0.9 | 2.3 ± 0.2 |
| Crab stage 4 | 29.4 ± 3.1 | 11.3 ± 1.5 | 2.7 ± 0.1 |
| Crab stage 5 | | | 3.2 ± 0.2 |

Table 8. *Hemigrapsus sanguineus*. Dry-weight growth (± SD; mg) of early juveniles. Dry weights are mg ± standard deviation. Day 0 designates the day of molting from the megalopa stage to crab stage 1. C-1 is crab stage 1, etc. n = number of individual crabs weighed. SD not calculated when n < 3

| Day | Stage | n | Dry weight |
|---|---|---|---|
| 0 | C-1 | 3 | 0.66 ± 0.04 |
| 5 | C-2 | 3 | 1.28 ± 10 |
| 15 | C-3 | 2 | 2.90 |
| 25 | C-4 | 2 | 4.65 |
| 35 | C-5 | 10 | 8.12 ± 1.95 |

nile crabs was approximately 650 µg (Table 8). This large increase over the dry weight of megalopae (see above) was probably due to uptake of calcium from the surrounding sea water as part of the calcification of the expanded carapace of the newly molted juveniles. After 35 d growth, juveniles had reached a mean dry weight of more than 8 mg (8000 µg); this represents a 12-fold increase in weight over a period of slightly more than a month.

### Spawning season and egg development

Most mature females were already carrying eggs when the study was initiated in early June, and gravid individuals were collected each week through the end of September (Table 9). Water temperature at the sampling site was approximately 15°C at the beginning of the study, increased to 26°C by late August, and fell to 15°C by late October. Carapace width of gravid females at the site ranged from 13 to 34 mm (mean = 20.0 ± 3.3 mm) during the study period. In the laboratory, females brooded eggs for a maximum of 14 d before hatching (25°C/30‰). Newly extruded egg masses were bright orange, gradually changed to dark brown, and then changed to brownish green as development proceeded. There was no significant effect of season on percentage of gravid females (ANOVA $F_{3,16}$, p = 0.37) or the percentage of females that were carrying early-stage eggs (ANOVA $F_{3,12}$, p = 0.43) during the months June to September; however, the percentage of gravid females rapidly declined to zero in October. Likewise, there was no significant effect of spring/neap cycle on either the proportion of gravid females (2-tailed *t*-test, df = 13, p = 0.92) or the percentage of females that were carrying early-stage eggs (2-tailed *t*-test, df = 12, p = 0.70). This result suggests that eggs hatch throughout the spring/neap cycle and corroborates a similar report from the native habitat of *Hemigrapsus sanguineus* (Saigusa & Kawagoye 1997).

Table 9. *Hemigrapsus sanguineus*. Periodicity of spawning. Collections were initiated on June 4 and continued at a weekly frequency until October 23. Values are mean percentages (± SD) of total number of crabs collected on each sampling day

| | % gravid | % early stage eggs |
|---|---|---|
| **Month** | | |
| June | 70 ± 8.7 | 38 ± 26.8 |
| July | 47 ± 16.7 | 55 ± 27.7 |
| August | 64 ± 7.9 | 39 ± 11.5 |
| September | 34 ± 13.0 | 20 ± 27.6 |
| October | 0.0 | 0.0 |
| **Tide** | | |
| Spring | 51 ± 18.4 | 50 ± 25.0 |
| Neap | 53 ± 19.4 | 47 ± 22.5 |

Microscopic examination of individual eggs (40×) showed that fertilized ova were almost entirely filled with yolk for the first 2 d of development. Only 75% of the yolk remained after 6 d, but no morphological structures were evident. After 8 d, 50% of the yolk had been utilized, and faint eye spots were visible. By Day 10, only 25% of the yolk remained, there were large black eyespots, and numerous pigmented areas were apparent. On Day 12 of development, there was very little yolk remaining, the segmented abdomen was visible in its entirety, and there was a visible heartbeat.

## DISCUSSION

Our results show that *Hemigrapsus sanguineus* is capable of development to the megalopa stage at salinities as low as 15‰. However, the ability of zoeal larvae to survive at reduced salinity was strongly modulated by temperature, and penetration to mesohaline regions of Middle Atlantic Bight estuaries would only be expected during July and August, when water tem-

peratures in the area typically exceed 20°C. Likewise, the tolerance of zoeal larvae to low temperature was affected by salinity, and zoeal larvae would most likely be excluded from low-salinity estuarine waters in those regions where summer temperatures do not rise above 20°C. This strong interaction between effects of temperature and salinity has been well documented for the zoeal larvae of several estuarine crabs (Costlow et al. 1962, Epifanio et al. 1988), including native species that co-occur with *H. sanguineus* in the Middle Atlantic Bight (e.g. the common mud crab *Panopeus herbstii*). But in contrast to the wide tolerances seen in the zoeal larvae of these species, the megalopa stage appears to have a more restricted set of requirements. For example, *H. sanguineus* failed to develop to the juvenile crab stage at temperatures below 20°C, and even at the most favorable conditions in our experiment (25°C/30‰) overall survival from hatching to the juvenile form was less than 20%. Costlow et al. reported similar results for *P. herbstii*, where survival from hatching to the juvenile stage fell from nearly 20% at 30°C to less than 5% at lower temperatures.

The duration of zoeal development for *Hemigrapsus sanguineus* was slightly longer than reported durations for co-occurring native mud crabs reared under similar conditions (e.g Epifanio et al. 1994, Welch & Epifanio 1995). This was attributable to the greater number of zoeal stages in *H. sanguineus* (5) compared to the various mud crab species (4). Specific growth rates (dry weight) of *H. sanguineus* were similar to published values for native mud crab species (Epifanio et al. 1994), and reached approximately 20% $d^{-1}$ under optimum conditions. However, newly hatched *H. sanguineus* were nearly twice as heavy as comparable mud crab zoeae, which, at exponential growth rates, yielded widely divergent dry weights at succeeding developmental stages. For example, newly molted *H. sanguineus* megalopae grew to approximately 200 µg compared to 75 µg for newly molted *Panopeus herbstii* megalopae (Welch & Epifanio 1995). Thus, the larvae of mud crab species such as *P. herbstii* may constitute suitably sized prey for the late developmental stages of the larger *H. sanguineus*.

Under laboratory conditions juvenile *Hemigrapsus sanguineus* underwent 4 molts in 35 d and, as expected, proportional growth (ca 8% of body weight $d^{-1}$) was considerably less than during larval development. Intermolt duration increased with each succeeding molt, but the rate of increase in carapace width was linear. This pattern of growth is similar to that seen with other brachyuran crabs (e.g. Van Heukelem et al. 1983, Dittel & Epifanio 1984). Newly metamorphosed juveniles had a mean carapace width of 1.6 mm and mean growth rate was approximately 0.06 mm $d^{-1}$. If we assume continued linear growth in carapace width (Van Heukelem et al. 1983), female crabs would reach maturity (15 mm) in approximately 7.5 mo. Because growth probably ceases during the coldest winter months, we might expect that crabs reach maturity about 1 yr after metamorphosis.

The wide range of sizes of gravid females in our field survey suggests that *Hemigrapsus sanguineus* may continue to molt after reaching maturity, and because egg brooding requires only 2 wk, females have the potential to produce several broods per year. Spawning of the Delaware Bay population spans at least 4 mo (June to September), which may allow populations of *H. sanguineus* to produce more broods each year than co-occurring populations of native species (e.g. *Dyspanopeus sayi*, *Eurypanopeus depressus*, *Panopeus herbstii*), which have considerably shorter reproductive seasons (Williams 1984).

Overall, the results of our study indicate that many of the early-life-history characteristics of *Hemigrapsus sanguineus* are well suited for dispersal along the east coast of the USA. For example, the zoeal stages have relatively wide tolerance for variation in environmental conditions and appear quite capable of survival in the mesohaline regions of estuaries or in the cool waters of the coastal ocean north of Cape Cod. This wide tolerance, combined with the extended spawning season of the adults, provides a broad temporal window for dispersal of the zoeal larvae. But counterbalancing this are the restricted set of requirements of the megalopa stage. Taken at face value, our results indicate that megalopae are incapable of development to the juvenile stage at temperatures much below 20°C or at salinities below 25‰. However, the wide latitudinal range of the species, both in North America and in its native habitat, suggests that megalopae under natural conditions may have somewhat wider tolerances. Indeed, it is important to recognize that laboratory studies of tolerance to factors like temperature and salinity are unable to mimic many characteristics of the natural environment that may have important effects on survival, development, and growth. Examples include diurnal cycles in water temperature (Christiansen & Costlow 1975), advection and turbulence (MacKenzie et al. 1990), and spatial distribution of prey organisms (Epifanio et al. 1994, Welch & Epifanio 1995). Thus, the results of this type of study are not to be taken literally; rather they provide a common metric by which to compare the relative abilities of different species to tolerate environmental variability.

*Acknowledgements*. The research was supported by funds from the University of Delaware Sea Grant College Program and from NSF grant OCE 9424146. We thank Rob Andrews, B-man Jones, Cecily Natunewicz, and Raymond Rodriguez for assistance with collection, culture, and data collection.

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*Editorial responsibility: Ron Kneib (Contributing Editor), Sapelo Island, Georgia, USA*

*Submitted: February 19, 1998; Accepted: June 12, 1998*
*Proofs received from author(s): August 10, 1998*