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The effect of starvation on acquisition of competence and post-metamorphic performance in the marine prosobranch gastropod *Crepidula fornicata* (L.)

Jan A. Pechenik*, Kimberly Hammer, Christopher Weise

Biology Department, Tufts University, Medford, MA 02155, USA

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Abstract

The duration of the precompetent period of development determines the obligate dispersal period for larvae of many benthic marine invertebrate species. This study considers the extent to which the onset of metamorphic competence in the gastropod *Crepidula fornicata* (L.) is controlled by growth rate or the attainment of a critical, threshold size. Precompetent larvae of *C. fornicata* were starved in filtered seawater for up to 6 days at 25°C and subsequently tested for competence by 5 h exposures to 20 mM excess K^+ in seawater. Control larvae were reared in excess phytoplankton suspension (*Isochrysis galbana*, clone T-ISO) and tested for metamorphic competence concurrently with starved individuals. Even though larvae stopped growing (and in fact lost up to 37% of their initial ash-free dry weight) after being transferred to filtered seawater, many individuals became competent to metamorphose while being starved. These results suggest an allocation of limited energy stores to differentiation rather than to growth, and clearly indicate that the onset of metamorphic competence is not size-dependent and does not depend on growth for larvae of this species. Metamorphosed juveniles grew more slowly if they had been starved as larvae, indicating a link between larval nutritional experience and post-metamorphic performance.

Keywords: Competence; *Crepidula*; Dispersal; Gastropod; Larvae; Metamorphosis; Starvation

1. Introduction

Strathmann et al. (1992) and Fenaux et al. (1994) have presented indirect but convincing evidence (for certain echinoid larvae) that rates of larval growth and morphological development are food limited at certain times of the year in temperate

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*Corresponding author. Fax: +1-617-6273805.

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zone coastal waters. Larval dispersal periods, however, depend not on growth rates per se, but on aspects of physiological development that need not depend on growth, specifically the duration of the precompetent period and the length of time that the larval period can be prolonged in the absence of the external cues typically required to initiate metamorphosis (reviewed by Crisp, 1974; Jackson and Strathmann, 1981; Scheltema, 1986; Pechenik, 1990; Tamburri et al., 1992). It is not yet clear what causes larvae to become competent to metamorphose. Previous studies (particularly with larvae of the gastropods *Crepidula fornicata* and *C. plana*) suggest that competence is not attained at any particular size threshold, and that the duration of the precompetent period can be uncoupled from growth rate by changes in temperature and salinity (Pechenik, 1984; Pechenik and Lima, 1984; Lima and Pechenik, 1985; Pechenik and Heyman, 1987; Zimmerman and Pechenik, 1991; Hansen, 1993). However, the degree to which the duration of the precompetent dispersal period is independent of growth rate has never been fully examined, and the effects of food limitation on the relationship have not previously been reported.

In this study we explored the effects of starvation on the duration of the precompetent dispersal period in the prosobranch gastropod *Crepidula fornicata* (L.). In particular we asked whether the larvae of *C. fornicata* can become competent to metamorphose without growing. We also considered the effects of limited starvation during larval life on post-metamorphic growth rates. To date, food limitation has been studied primarily with regard to its effects on larval survival, growth, and morphological development (reviewed by Pechenik, 1987; Olson and Olson, 1989; Hart and Strathmann, 1994; Boidron-Métairon, 1995; Morgan, 1995).

2. Materials and methods

2.1. *Influence of food concentration on the onset of metamorphic competence and post-metamorphic growth*

Seawater (about 30 ppt S) was passed through a 1 μm cartridge filter at Northeastern University's marine laboratory (Nahant, MA, USA) and stored at 10°C until needed. Adult *Crepidula fornicata* were obtained from Woods Hole, MA, USA on February 8, 1994 and maintained at room temperature (ca. 23°C) on a mixed diet of the naked flagellates *Isochrysis galbana* (clone T-ISO) and *Dunaliella tertiolecta* (clone DUN) for about two and-a-half weeks, until larvae were released from one female (day 0). Larvae (and metamorphosed juveniles) were then maintained at 25°C for the rest of the experiment. Larvae were reared in batch culture at 25°C (12L:12D photoperiod) on *I. galbana* at 18×10^4 cells ml^{-1} for four days before experiments were initiated; *I. galbana* at this concentration supports rapid growth of *C. fornicata* with low mortality through metamorphosis (Pechenik, 1980, Pechenik, 1984; Pechenik et al., 1996a). Seawater was forced through a 0.45 μm cartridge filter before use. Larvae were transferred to new food and water at the second and fourth days of batch culturing.

On day 5, we transferred larvae in groups of 12 into 20 glass dishes (8 cm diameter) containing 45 ml of *I. galbana* suspension at 18×10^4 cells ml^{-1}. Two days after transferring larvae to glass dishes (day seven) we measured all larvae in eight replicates to determine whether there were any significant differences in mean larval shell lengths among dishes. Larval shell lengths were measured non-destructively as follows. A larva was pipetted onto a microscope slide in a small volume of water. Excess water was quickly removed by pipet to immobilize the larva on its left side. Shell length was then determined at ×50 using an ocular micrometer and the larva was immediately returned to its container.

On day 8, larvae in five dishes (12 larvae per dish) were exposed for 5 h to 20 mM excess potassium (as KCl) in seawater to determine percent competence (Pechenik and Heyman, 1987; Pechenik and Gee, 1993). No larvae metamorphosed. The larvae were then transferred to seawater that had been passed through a 0.45 μm membrane filter (Millipore, Bedford, MA, USA). Additional groups of larvae (five replicates each time) were tested for competence on days nine and ten, and those larvae that failed to metamorphose were transferred to 0.45 μm filtered seawater. In this way, groups of precompetent larvae were starved at different ages. Each treatment group consisted of five replicates with 12 larvae per replicate. Larvae were changed to fresh phytoplankton suspension (control larvae), or filtered seawater in clean glass dishes daily. Note that all larvae were well-fed for seven days before any were transferred to filtered seawater.

Control larvae maintained at full ration throughout the experiment were tested for metamorphic competence on day 11. Starved larvae were tested for competence on days 11 and 14 and the shell lengths of all individuals, whether or not they metamorphosed, were measured at ×50. Through this design, larvae were tested for competence after 0–6 days of starvation. For example, larvae starved beginning on day 8 were tested for competence three and six days later (on days 11 and 14, respectively) while those starved beginning on day 9 were tested for competence two and five days later (again, on days 11 and 14, respectively).

A haphazardly selected subsample of metamorphosed individuals ($n=55$) was maintained individually at full ration in 45 ml of phytoplankton suspension (T-ISO) at 25°C and remeasured at ×50 after three days to determine post-metamorphic growth rates; phytoplankton suspension was replaced daily during this time.

2.2. Influence of starvation on larval shell growth and biomass

Larval shell lengths were measured in all treatment groups just before larvae were transferred to filtered seawater on days 8–10. All individuals were remeasured on days 11 and 14, after testing for metamorphic competence.

The effect of starvation on larval biomass was assessed in a separate experiment, by destructive sampling. Larvae obtained from a different female were reared at full ration (1.8×10^5 cells ml^{-1}) for 4 days at 25°C, and then transferred to 0.45 μm filtered seawater for an additional two or four days to determine weight loss during starvation. Three groups of larvae were prepared for weighing at the beginning of the starvation period to determine initial larval weights; other larvae were prepared for weighing after the two-or four-day starvation period. Control larvae were maintained at full ration for the full eight days and then prepared for weighing. Four groups of larvae were weighed for each treatment group, with 10–14 larvae per group.

To prepare larvae for weighing, they were rinsed briefly in distilled water and transferred to paper towel. They were then picked up individually at the end of a pin and counted into preweighed foil containers holding a small volume of distilled water; the distilled water facilitates transfer of larvae to the containers without altering dry container weight (Pechenik, 1978). Samples were then dried at 60°C for 24–48 h, weighed on a Cahn Model 21 electrobalance to the nearest μg, ashed for 5 h at 525°C, and reweighed to determine tissue biomass from the weight lost during ashing (Paine, 1964; Pechenik, 1980).

2.3. Data analyses

Data were analyzed by standard parametric statistical procedures unless assumptions about equal standard deviations among treatment groups failed Bartlett's Test for homogeneity of variances. In those cases, data were analyzed by Kruskal-Wallis nonparametric analysis of variance (ANOVA).

3. Results

3.1. Adequacy of culture conditions

No larvae died during these experiments, although a few individuals (never more than 5% in any experiment) were lost, or were damaged in routine handling and subsequently discarded.

Larvae used in the main experiment emerged at a mean shell length (±SD) of 403.8 μm±23.6 ($n=27$), and grew at about 85 μm day^{-1} at full ration. This is comparable to growth rates reported previously for larvae of this species reared at similar temperatures (Pechenik, 1984; Pechenik and Lima, 1984). There were no significant differences ($P>0.05$, one-way analysis of variance) in mean larval shell lengths in all dishes, based on measurements made just before larvae were transferred to filtered seawater. Thus, all larvae were growing at comparable rates in all dishes before any were starved.

3.2. Influence of starvation on larval shell length and biomass

Mean larval shell lengths following 1–6 days in filtered seawater never differed significantly from mean larval shell lengths at the start of the starvation period ($P>0.05$, t-test; Fig. 1). Larvae starved beginning on day 9, for example, were triggered to metamorphose two days later (on day 11) and five days later (on day 14); the 43 individuals that metamorphosed were the same size, on average, as individuals measured just before their transfer to filtered seawater (Fig. 1). Both biomass and protein content increase linearly with shell length in this species (Pechenik, 1980, Pechenik, 1984) so that changes in shell length accurately reflect growth. Thus, larval growth ceased abruptly once larvae were transferred to filtered seawater.

Larvae transferred to filtered seawater lost weight at a constant rate of about 1.7 μg day^{-1} over a four-day period (Fig. 2). This agrees well with the rate of weight loss

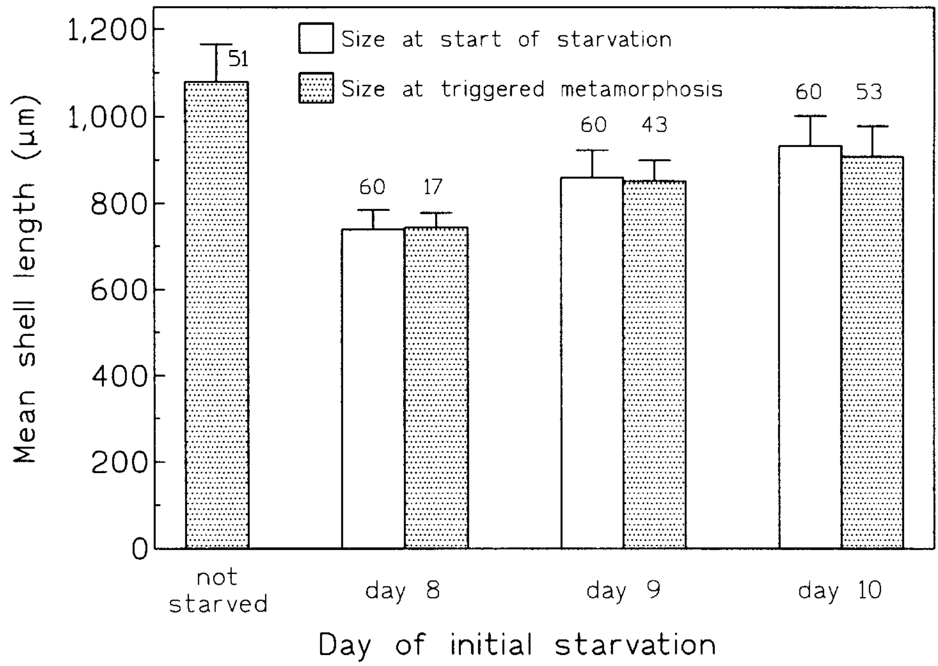

Fig. 1. Effect of starvation on larval growth. Larvae of *Crepidula fornicata* were reared on *Isochrysis galbana* (clone T-ISO) at 1.8×10^5 cells ml^{-1} and transferred to 0.45 μm filtered seawater on the days indicated. Larvae were later tested for metamorphic competence on day 11 (control larvae) or on days 11 and 14 (starved larvae). The total number of individuals measured in each treatment is indicated above each bar; for starved individuals, this is the total number of individuals that metamorphosed on days 11 and 14, after 1–6 days of starvation. Larvae transferred to filtered seawater on day 10, for example, experienced one day of starvation by day 11 and three days of starvation by day 14. Error bars represent one SD about the mean shell length.

predicted from previously collected respiration data. If we assume that carbon content is 50% of dry tissue weight (Nichols, 1975) and assume a respiratory quotient (RQ) of 0.8 (Brody, 1945), the rate of weight loss that we documented would require a respiration rate of 5.7×10^{-2} μl O_2 h^{-1}. This is in good agreement with respiration rates reported for larvae of this species by Dobberteen and Pechenik (1987): about 8.5×10^{-2} μl O_2 h^{-1} for 800 μm larvae reared at 24°C.

3.3. Effects of food limitation on age at metamorphic competence, size at competence, and post-metamorphic growth rates

Larvae were able to gain metamorphic competence for at least six days following their transfer from 18×10^4 cells ml^{-1} to filtered seawater (Fig. 3). For example, no larvae were competent to metamorphose when tested on day 9; yet more than 30% of larvae that were starved beginning on day 9 attained competence by day 11 and substantially more larvae in this treatment group became competent over the next three days of starvation (open triangles). In other words, the number of larvae starved since day 9 and

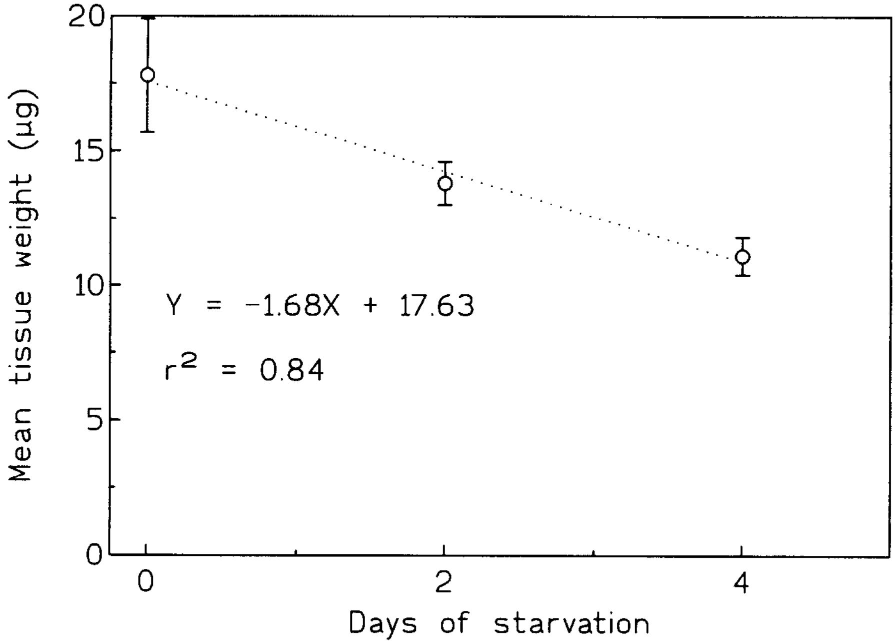

Fig. 2. Rate of weight loss (ash-free dry weight) for *Crepidula fornicata* larvae maintained in 0.45 µm filtered seawater at 25°C. Each point represents the mean of four replicates, with 10–14 larvae weighed per replicate.

metamorphosing on day 14, after five days of starvation, was significantly greater than the number of larvae metamorphosing on day 11 after only two days of starvation (Mann-Whitney two sample test: $U = 1.0$, $P = 0.005$). Starvation did, however, increase the average age at which larvae in each population became competent (compare day 11 data across all treatments).

Starvation significantly ($P < 0.05$, Kruskal-Wallis nonparametric ANOVA) reduced the size at which the average larva metamorphosed, from about 1100 µm for control larvae induced to metamorphose on day 11 to about 750 µm for larvae induced to metamorphose on days 11 and 14, after having been starved for up to six days (Fig. 4). Mean shell lengths of competent larvae were statistically equivalent ($P > 0.05$, Dunn's multiple comparisons test) only for larvae that were starved beginning on days 9 and 10.

Larval shell length was an inadequate predictor of metamorphic competence whether larvae were continuously fed or starved before metamorphosis was triggered, and starvation greatly decreased the average shell length at which larvae were induced to metamorphose (Fig. 5). Larvae that were fed continuously metamorphosed over a wide range of shell lengths; all individuals exceeding about 1200 µm in shell length metamorphosed when exposed for 5 h to 20 mM excess K^+, but size was an unreliable indicator of competence for smaller individuals (Fig. 5A). In contrast, for larvae that had been starved for two days before testing, no more than about 50% of the individuals in any size category were induced to metamorphose by excess K^+; moreover, the largest of these individuals (900–1000 µm) were actually less likely to metamorphose than larvae

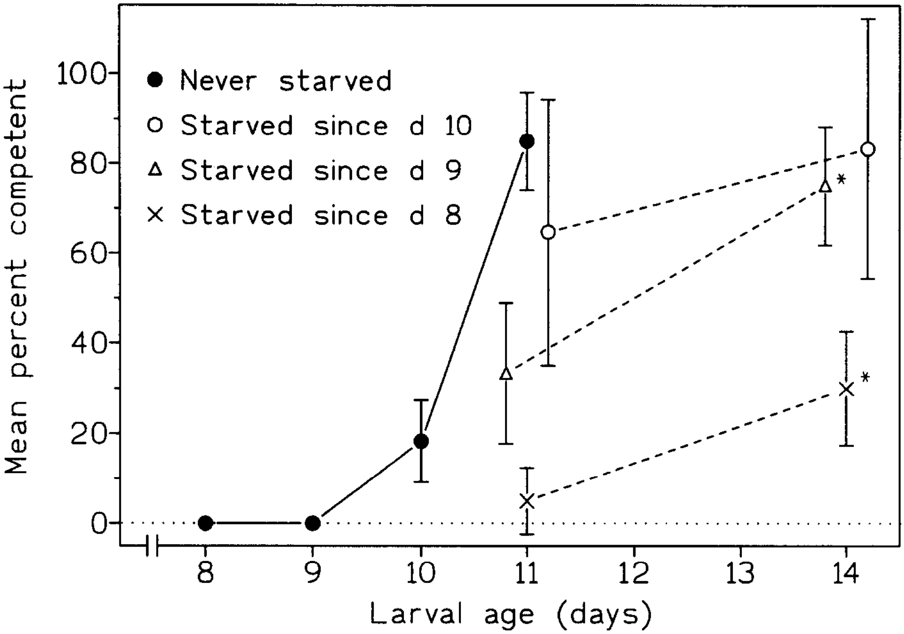

Fig. 3. Influence of starvation on the ability of *Crepidula fornicata* larvae to become metamorphically competent at 25°C. Control larvae were reared at high phytoplankton concentration (1.8×10^5 cells ml^{-1}) throughout the experiment, and tested for competence on day 11. Other larvae were transferred to 0.45 μm filtered seawater on days 8, 9 or 10 and tested for competence twice, on days 11 and 14. Each point represents the mean percent metamorphosis in five replicates, with 12 larvae per replicate. Data points for days 11 and 14 are displaced slightly to improve clarity. Error bars represent one SD about the mean. *Significant difference between means on days 11 and 14 (Mann-Whitney two sample test).

of intermediate shell length (800–900 μm), Fig. 5B. Comparable data (not shown) were obtained for larvae starved beginning on days 8 and 10.

Larvae that became competent to metamorphose after having been starved for more than about two to three days metamorphosed into slower growing juveniles (Fig. 6).

4. Discussion

The larvae of benthic marine invertebrates must typically develop for a time in the plankton before becoming capable of metamorphosing to juvenile form and habitat; this precompetent period of development defines the obligate dispersal period for the species (reviewed by Pechenik (1990)). It is not clear what causes larvae to become competent. Competence most likely results from the secretion or activation of receptor proteins in specific receptor cells at the larval surface, the completion of particular neural pathways, the activation of particular neurosecretory systems, or the activation of receptor systems on target tissues (Hadfield, 1978; Highnam, 1981; Trapido-Rosenthal and Morse, 1986). Despite this probable role of differentiation in establishing the onset of metamorphic

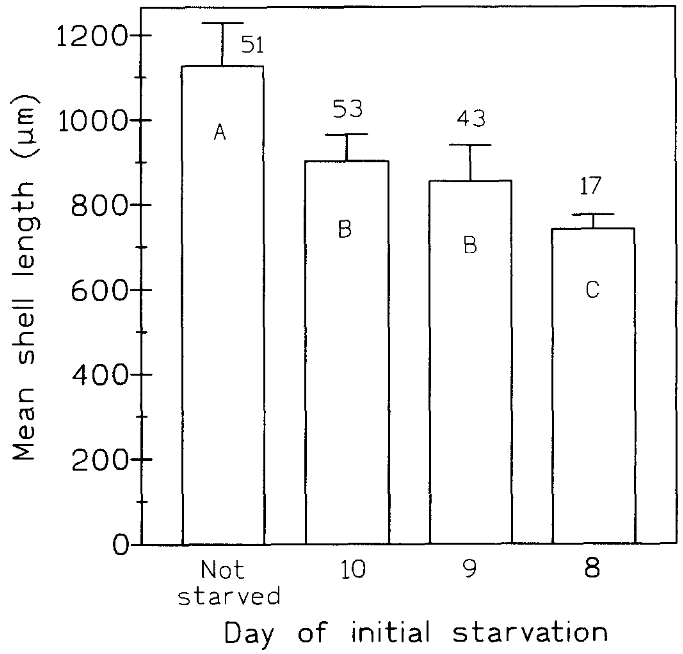

Fig. 4. Influence of starvation on mean shell length at metamorphosis. Metamorphosis was triggered on days 11 and 14 by exposing larvae for 5 h to 20 mM excess K^+ in seawater. Numbers above the bars indicate number of individuals measured for each treatment. Means that do not differ significantly from each other display the same letter within the bar. Error bars represent one SD about the mean.

competence, the predicted duration of precompetent development is commonly linked to rates of larval growth for planktotrophic larvae (e.g., Scheltema, 1967, Scheltema, 1986; Vance, 1973a, Vance, 1973b; Qian et al., 1990; Jonsson et al., 1991; Widdows, 1991; Dekshenieks et al., 1993; Inestrosa et al., 1993; Beiras et al., 1994; Fenaux et al., 1994; Raby et al., 1994; Tremblay et al., 1994). Recent studies have clearly shown, however, that size and age are inadequate predictors of metamorphic competence for larval gastropods and bivalves (Eyster and Pechenik, 1987; Coon et al., 1990; Mullineaux and Butman, 1991; Bachelet et al., 1992; Grassle et al., 1992; Snelgrove et al., 1993), and that growth rate can be a poor predictor of duration of the precompetent period (Zimmerman and Pechenik, 1991; Hansen, 1993). A direct correspondence between larval growth rate and duration of the precompetent period has been demonstrated only for larvae of the polychaete *Phragmatopoma californica*, over a temperature range of 15–20°C (Pawlik, 1988). Moreover, lecithotrophic larvae routinely attain metamorphic competence without growing (e.g., Switzer-Dunlap and Hadfield, 1977; Woollacott et al., 1989; Pechenik and Cerulli, 1991; Miller, 1993), so becoming competent clearly does not require growth, although it must require differentiation.

In the present study, we have completely uncoupled the onset of competence from growth in *Crepidula fornicata*. There was no detectable shell growth after larvae were

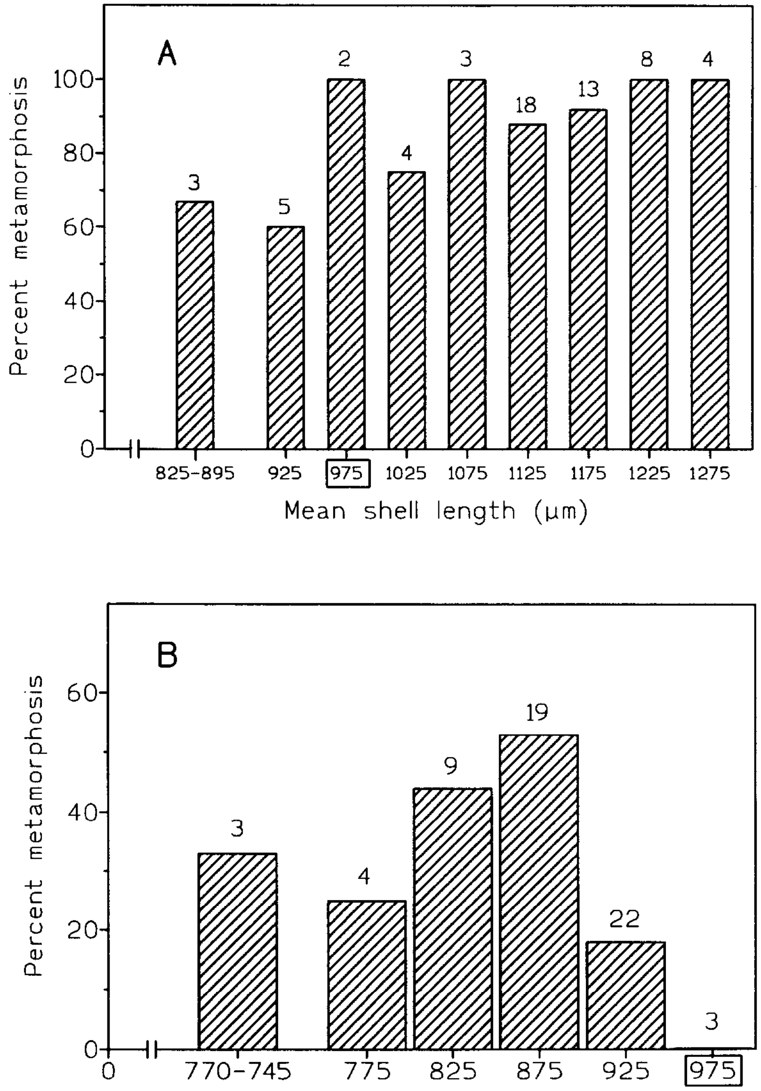

Fig. 5. Influence of starvation on the extent to which larval shell length indicates metamorphic competence in *Crepidula fornicata.* Larvae were induced to metamorphose on day 11, either after being reared at continuously high phytoplankton concentration (A) or two days after being transferred to filtered seawater (B). The number of individuals tested in each size category is indicated above each bar. The rectangles on the *x*-axes indicate corresponding size classes for the two panels.

transferred to filtered seawater; indeed, larvae lost weight in filtered seawater, so that at the end of four days average ash-free dry weight was only about 63% of initial weight. In contrast, Pilkington and Fretter (1970) reported that veligers of *C. fornicata* grew

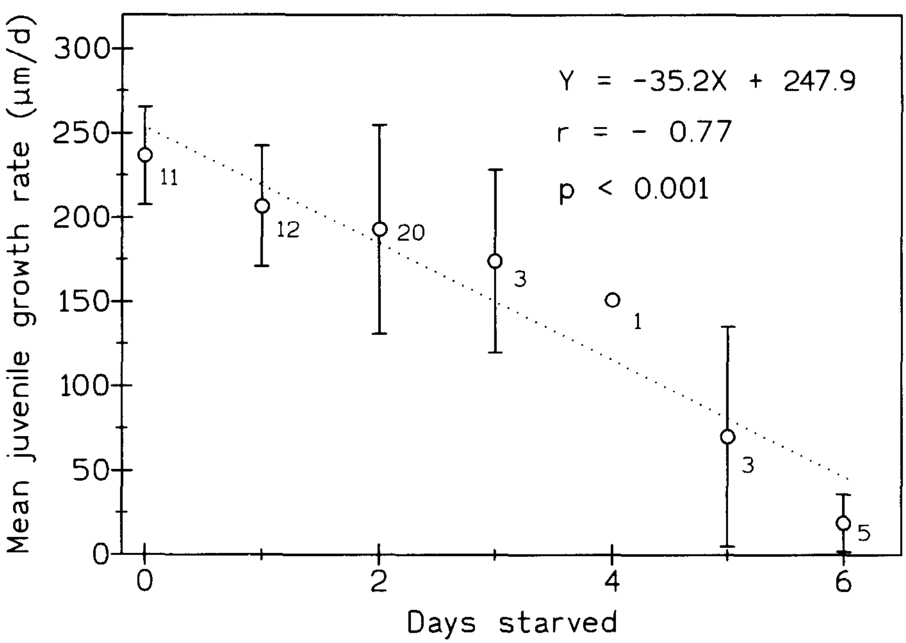

Fig. 6. Influence of starvation during larval life on postmetamorphic growth of *Crepidula fornicata* at 25°C. Larvae were starved up to six days and triggered to metamorphose by elevating seawater K^+ concentration by 20 mM. Metamorphosed individuals were haphazardly subsampled and then maintained at full ration (1.8×10^5 cells ml^{-1}). Juveniles were measured at metamorphosis and again three days later to assess growth rate. The numeral to the right of each circle indicates the number of individuals in that treatment group (total $n = 55$ individuals). Error bars represent one SD about the mean.

during three weeks without food. It seems likely that particulate food was present in their larval cultures, however, as they removed particulates by passing water through a 3 µm mesh.

Despite the absence of shell growth and the loss of biomass in our experiments, larvae became competent to metamorphose for at least 4–6 days following their transfer to filtered seawater. Starved larvae, in our experiments, achieved competence at the low end of the size range reported previously for fully-fed individuals of this species (Zimmerman and Pechenik, 1991; Pechenik et al., 1996a). Although we cannot discount the possibility of a minimum size below which larvae of *C. fornicata* cannot become competent, acquisition of metamorphic competence in this species is clearly controlled neither by rate of growth nor by the attainment of any particular size or weight. To date, size-triggered metamorphosis or competence for metamorphosis has been convincingly demonstrated only for the larvae of some insect species (e.g., Nijhout, 1975, Nijhout, 1984; Blakley, 1981). Wilbur and Collins (1973) proposed that amphibian larvae become capable of metamorphosing at a particular size, but experiments have yet to confirm that hypothesis (Smith-Gill and Berven, 1979; Hensley, 1993; Leips and Travis, 1994). For larvae of benthic marine invertebrates, decreases in food concentration typically increase the duration of the planktonic period, but not necessarily in proportion to their effects on growth rate (Zimmerman and Pechenik, 1991; Hansen, 1993).

The impact of starvation on larval development has been studied primarily for crustaceans (reviewed by Olson and Olson, 1989), with a focus on defining critical periods of development during which starvation prevents successful metamorphosis to the next larval stage (e.g., Anger et al., 1981; Dawirs, 1983, Dawirs, 1984; Anger, 1987, Anger, 1995; Wehrtmann, 1991). Non-crustacean larvae are known to tolerate long periods of starvation quite well (Thorson, 1950; Loosanoff, 1954; Bayne, 1965; Millar and Scott, 1967; Perron and Turner, 1977; His et al., 1989; Allison, 1994; Pawlik and Mense, 1994; Boidron-Métairon, 1995; Eckert, 1995), although an effect of temporary starvation on larval growth capacity has been reported for the bivalve *Crassostrea gigas* (His and Seaman, 1992). In addition, the larvae of one bivalve and several echinoderm species have been shown to increase the length of food collecting devices as an apparent adaptation to food limitation (Boidron-Métairon, 1988; Fenaux et al., 1988; Strathmann et al., 1993; Hart and Strathmann, 1994), but the impact of starvation or food limitation on the onset of metamorphic competence has not been widely investigated. Larvae of the opisthobranch *Doridella obscura* died without ever becoming competent to metamorphose when they were starved from the time of hatching (Perron and Turner, 1977). Similarly, starving precompetent larvae of the asteroid *Asterina miniata* typically forestalled all further development (Allison, 1994). Food-limiting (no larvae were actually starved) the larvae of the echinoid *Dendraster excentricus* delayed development of the juvenile rudiment and, as with *C. fornicata* larvae, resulted in small juvenile sizes at metamorphosis (Hart and Strathmann, 1994; but see also Paulay et al. (1985) for opposing results). Although the impact of starvation on precompetent larvae of the polychaete *Phragmatopoma lapidosa californica* has not yet been reported, competent larvae reverted to a precompetent state when starved for several days (Pawlik and Mense, 1994); that is, they lost the ability to metamorphose in response to chemical cues, suggesting that precompetent larvae of these species would probably not attain competence if starved.

Larvae of *Crepidula fornicata* seem unusual for planktrotrophs in their ability to achieve metamorphic competence when fully deprived of food, and in the complete absence of growth; energy reserves were apparently allocated to differentiation rather than to growth. A similar response has recently been reported for larvae of the echinoid *Encope michelini*, which, if fed early in development and then starved, successfully metamorphosed during the period of starvation (Eckert, 1995). The adaptive significance of this response to starvation is considered in another paper (Pechenik et al., 1996b). Anger (1995) reports a related result for the crab *Sesarma curacaoense*. In his experiments, starvation generally increased the duration of the second zoeal stage in proportion to the number of days starved, as reported for other crustaceans (e.g., Anger et al., 1981; McConaugha, 1985; Wehrtmann, 1991). However, in one of his experiments continual starvation shortened the duration of the second zoeal stage, which he attributed to a switch of energy allocation from growth to accelerated morphogenesis.

Starving precompetent larvae of *C. fornicata* had an unexpected effect on juvenile growth rates, which were reduced in proportion to the number of days that larvae were starved even though all juveniles were transferred to full ration immediately after metamorphosis. This reduced juvenile growth was not likely an artifact of exposure to excess K^+ (Eyster and Pechenik, 1988; Davis et al., 1990). More likely, starvation in the larval stage compromised either the juveniles' ability to collect food particles or their ability to digest collected food particles efficiently.

Our data extend previous findings that some larval experiences can compromise post-metamorphic performance. In particular, delaying larval metamorphosis in the laboratory correlated with reduced rates of post-metamorphic growth or development in the barnacle *Balanus amphitrite* (Pechenik et al., 1993) and several bryozoan species (Nielsen, 1981; Woollacott et al., 1989; Orellana and Cancino, 1991). As reported by Highsmith and Emlet (1986), delayed individuals of the echinoid *Dendraster excentricus* also tended to grow more slowly than control individuals following metamorphosis, although the differences were not statistically significant; juvenile survival was, however, substantially reduced for individuals that were forced to delay metamorphosis, as it was for unfed larvae of the gastropod *Phestilla sibogae* (Miller, 1993). Similarly, although delaying metamorphosis of the polychaete *Capitella* sp. I did not affect mean rate of post-metamorphic growth or time to reproductive maturity, it did reduce post-settlement survival dramatically (Pechenik and Cerulli, 1991). These findings were not anticipated in Thorson's (Thorson, 1950) landmark discussion of 'waste' during development and violate an important assumption incorporated into models of reproductive pattern evolution (Vance, 1973a, Vance, 1973b; Christiansen and Fenchel, 1979; Roughgarden, 1989) — that starvation during the larval period and increased length of larval life have no impact on post-metamorphic performance. Yet the extent to which the larvae of benthic marine invertebrates delay their metamorphosis or experience food limitation during development in the field clearly has the potential to influence post-metamorphic survival, either directly or indirectly. Possible indirect effects include increasing the vulnerability of juveniles to predation, through decreased size at metamorphosis and slower rates of post-metamorphic growth, and reducing the ability of juveniles to compete successfully for food or space following metamorphosis, by slowing post-metamorphic growth rates.

These results also have interesting implications for the transport of larval stages to non-native habitats in ship ballast water. Deprived of new primary production and appropriate metamorphic substrate for days or weeks in ship ballast (Carlton and Geller, 1993), entrained phytoplanktotrophic larvae may experience extended periods of food deprivation and delayed metamorphosis. Our results indicate that, for at least some species, the ability of individuals to thrive as juveniles and accomplish a successful invasion after discharge may be markedly compromised as a consequence.

Acknowledgments

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