Metamorphosis Is Not a New Beginning

Larval experience influences juvenile performance

Jan A. Pechenik, Dean E. Wendt, and Jeremiah N. Jarrett

Many marine invertebrate species have complex life cycles, in which one or more free-living developmental stages eventually metamorphoses to a morphologically—and often ecologically and physiologically—distinct juvenile stage. Such life cycles are also common among insects, amphibians, and marine fishes. Among marine invertebrates, complex life cycles are widely distributed among such diverse animals as sponges; turbellarian and trematode flatworms; gastropod and bivalved mollusks; polychaete worms; lobsters, crabs, barnacles, and other crustaceans; bryozoans; and echinoderms (Thorson 1950). Marine invertebrate larvae may feed on phytoplankton and other particulates or subsist entirely on yolk or other nutrients provided by the mother. They may spend as little as a few minutes or as long as several to many months in the plankton before metamorphosing to adult form and habitat (Pechenik 1990).

Marine invertebrate larvae are microscopic, using either cilia or specialized appendages to swim and, for feeding individuals, to collect food. As with the larvae of at least some fish species (Victor 1986, Sweatman 1988, Cowen 1991, Sponaugle and Cowen 1994), the larvae of most marine invertebrates become physiologically competent to metamorphose during development but do not necessarily metamorphose at that time (Figure 1; Pechenik 1990). Instead, metamorphosis occurs only after competent larvae encounter certain environmental cues that are associated with habitat appropriate for the juvenile (Pechenik 1990, Pawlik 1992). Following convention (Scheltema 1961, Crisp 1974) we refer to this retention of larval form after the onset of competence as "delayed metamorphosis."

Only recently have biologists considered the impact that larval experience can have on postmetamorphic vulnerability to environmental stresses

It is not yet clear whether larvae actively delay their metamorphosis, for example by secreting some substance that inhibits metamorphosis in the absence of particular external cues, or whether the metamorphic pathway is simply not stimulated until the appropriate cue(s) is encountered (Pechenik and Qian 1998). In any event, delayed metamorphosis is not a developmental arrest analogous to insect diapause (Nijhout 1994). Rather, competent marine invertebrate larvae remain active in the plankton, often continuing to feed and grow (Pechenik 1990). During this time, the larval form and lifestyle may be maintained for days, weeks, or even months (Pechenik 1990), allowing larvae of some species to disperse across entire ocean basins (Scheltema 1971).

Although delayed metamorphosis is known primarily from laboratory studies, there is at least indirect evidence that marine invertebrate larvae also delay their metamorphosis in the field (Scheltema 1971, Pechenik 1990). Despite several decades of active research, biologists understand little about what makes larvae competent to metamorphose or what determines how long they can delay metamorphosis, nor do we fully understand the sequence of events that occurs internally once the external stimulus for metamorphosis is perceived (Degnan and Morse 1995, Cooper and Leise 1996, Pechenik and Qian 1998).

In marine species with complex life cycles, adult population size depends to a large extent on the transport of larvae into and away from adult populations (Thorson 1950, Jackson and Strathmann 1981, Bailey and Houde 1989, Hill 1991, Shanks 1995, Alexander and Roughgarden 1996), the number of larvae that

Jan A. Pechenik (e-mail: jpecheni@emerald.tufts.edu) is a professor in the Biology Department of Tufts University, Medford, MA 02155. Dean E. Wendt (e-mail: dwendt@oeb.harvard.edu) is a graduate student in the Department of Organismic and Evolutionary Biology at Harvard University, Cambridge, MA 02138. Jeremiah N. Jarrett (e-mail: jarrettj@ccsu.edu) is an assistant professor in the Department of Biological Sciences at Central Connecticut State University, New Britain, CT 06050-4010.

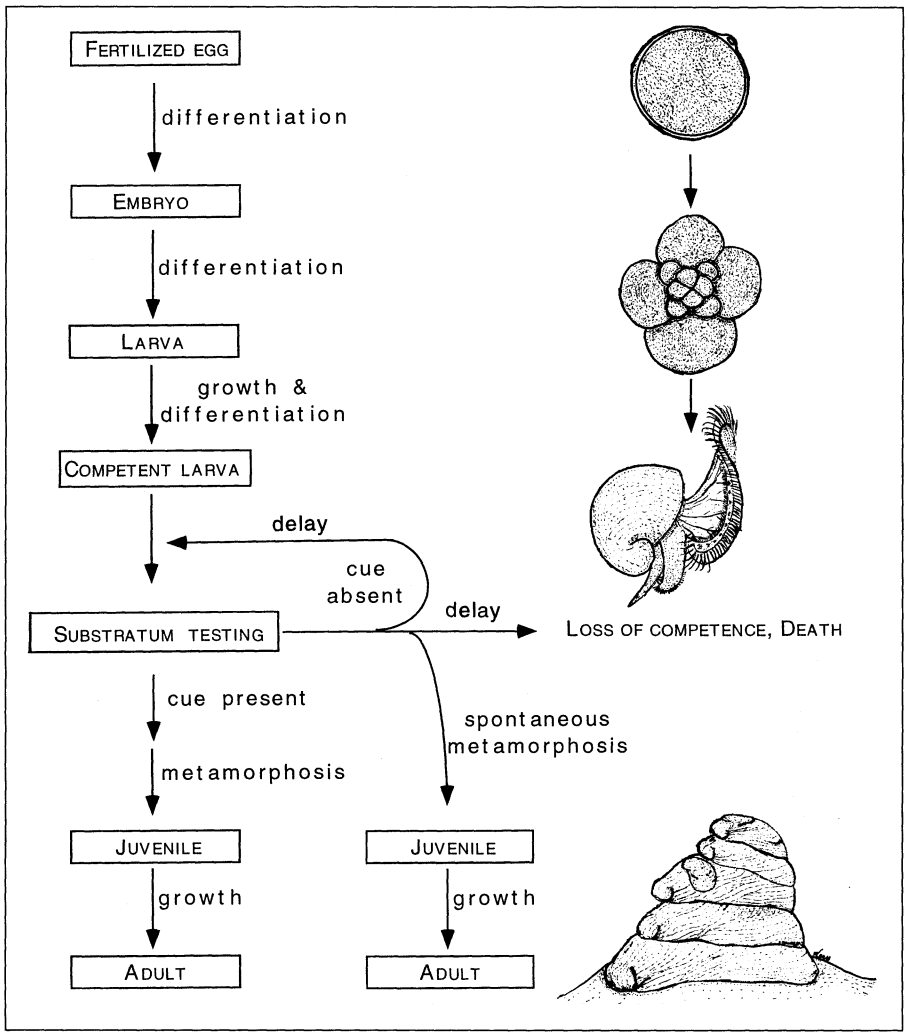

Figure 1. Complex life cycle of a typical marine invertebrate. Larvae develop for a time in the plankton before becoming competent to metamorphose. Metamorphosis is triggered by contact with chemical or physical cues that are typically associated with the appropriate juvenile habitat. The larva at the right is a veliger of the gastropod *Crepidula fornicata* (slipper shell snail). The suspension-feeding adults of this species aggregate to form stacks, as shown. Gastropod veligers are typically 250–750 μm in shell length.

survive to metamorphose (Thorson 1950, Istock 1967, Bailey and Houde 1989, Berven 1990, Kerrigan 1996), and the extent of postmetamorphic mortality (Gosselin and Qian 1997, Hunt and Scheibling 1997). Many studies have considered the roles of predators, temperature, food conditions, pollutants, and other environmental factors on larval mortality (reviewed by Pechenik 1987, Young and Chia 1987, Bailey and Houde 1989, Morgan 1995) and the influence of various biological and physical stresses on juvenile mortality (reviewed by Gosselin and Qian 1997, Hunt and Scheibling 1997). However, only recently have biologists considered the impact that larval experience can have on postmetamorphic vulnerability to these stresses.

In hindsight it should come as no surprise that experiences in one part of marine invertebrate development can influence the performance of later stages. It is well known, for example, that various stresses experienced early in the development of mammalian embryos can affect many aspects of postbirth performance, including enzyme function, learning capacity, behavior, and the likelihood of coronary heart disease and obesity (Ravelli et al. 1976, Barker 1995, Rice 1996a, 1996b, Desai and Hales 1997). Similarly, incubation temperature and humidity have been shown to influence hatching size, growth rates, locomotory ability, behavior, and juvenile survival in some reptiles (Miller et al. 1987, Janzen and Paukstis 1991, Janzen 1995, O'Steen 1998), and poor food conditions early in development can influence both survival and fecundity in birds (Haywood and Perrins 1992, Merilä and Svensson 1997). Even the prolonged storage of plant seeds can reduce the tolerance of seedlings to environmental stress (Priestly 1994).

But such effects of early experience on later performance have generally not been sought among marine species with complex life cycles, possibly because either the larval stage or the juvenile stage of many species is difficult to maintain in the laboratory or monitor in the field. In addition, the lack of such studies may reflect the general view of metamorphosis as a new beginning: a morphological, ecological, and physiological revolution followed by a fresh start with a new body and a new lifestyle in a new habitat. In this article, we review the evidence that certain larval experiences can limit postmetamorphic performance in a variety of marine invertebrates, consider some of the mechanisms through which the effects may be mediated and some of the ramifications of those effects, and suggest directions for future research. Although we focus on marine invertebrates, we also include studies on insects, amphibians, and fishes to emphasize the apparent generality of the phenomenon: Metamorphosis is not necessarily a new beginning.

Larval feeding influences postmetamorphic performance

Many marine invertebrate larvae probably experience fluctuations in both food quantity and food quality (Pechenik 1987, Fenaux et al. 1994, Morgan 1995) because of the patchy distribution of phytoplankton in both space and time (e.g., Cowles et al. 1993). Although effects of low food concentrations and poor food quality on larval growth and survival have been well documented for the larvae of many marine invertebrate species (reviewed by Pechenik 1987, Boidron-Métairon 1995, Morgan 1995), few studies have considered that food limitation experienced dur-

ing larval life might interfere with postmetamorphic performance.

Such detrimental effects on juvenile growth potential have recently been documented for a marine gastropod, the slipper shell snail (*Crepidula fornicata*; Figure 1). This snail feeds on suspended phytoplankton both before and after metamorphosis, so that all stages in the life cycle can be reared in the laboratory on the same diet; larvae capture food particles using a specialized ciliated organ (the velum) that is lost at metamorphosis, whereas juveniles capture particulate food using ciliated gills. Transferring larvae of *C. fornicata* from seawater with a high phytoplankton concentration (18×10^4 cells/ml of *Isochrysis galbana*, clone T-ISO) to either filtered seawater or to seawater with a dramatically lower concentration of phytoplankton (1×10^4 cells/ml or less) for several days significantly reduced average juvenile growth rates, even though individuals were transferred back to the high phytoplankton concentration after metamorphosis (Pechenik et al. 1996a, 1996b).

Juvenile growth rates were reduced even when larvae were starved for only a few days very early in development and then returned to control conditions for the next 8 days before metamorphosis. Although growth rates of starved larvae soon returned to those of control individuals, juvenile growth rates for at least the first 3–4 days after metamorphosis were significantly below those of control individuals that had never been starved as larvae (Figure 2). Thus, even short periods of reduced food availability during larval life may constrain juvenile growth rates, potentially increasing vulnerability to predators and altering key life history characteristics (Gosselin and Qian 1997).

Duration of larval life affects juvenile performance

The functional and temporal separation between becoming competent to metamorphose and the actual process of metamorphosis has long been viewed as beneficial: The ability to delay metamorphosis in the absence of specific environmental cues increases the likelihood that individuals will enter habitats that are most likely to support growth and survival into adulthood (Thorson 1950, Morgan 1995). A growing body of evidence suggests, however, that delaying metamorphosis can increase postsettlement mortality or reduce the juveniles' ability to compete successfully for space or food (Woollacott et al. 1989, Pechenik and Cerulli

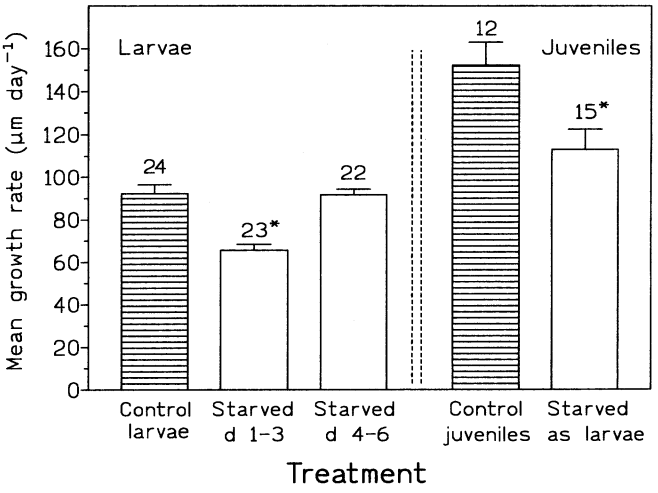

Figure 2. The influence of short-term starvation during larval life on subsequent larval and juvenile growth rates at 25 °C in the slipper shell snail, *Crepidula fornicata*. One day after hatching, some larvae were starved for 3 days and then returned to a diet of phytoplankton (18×10^4 cells/ml). Larval shell lengths were measured at the end of the starvation period, 3 days after return to the phytoplankton diet, and 3 days after that; thus, larval growth rates could be calculated for days 1–3 and days 4–6 after larvae were returned to the phytoplankton suspension. Control individuals were always reared at high phytoplankton concentrations (18×10^4 cells/ml). Asterisks indicate means that differ significantly ($P < 0.05$) from the corresponding control means. Juvenile growth rates were determined for the first 4 days after metamorphosis. Unpublished data from Jan Pechenik, Jeremiah Jarrett, and Jen Rooney.

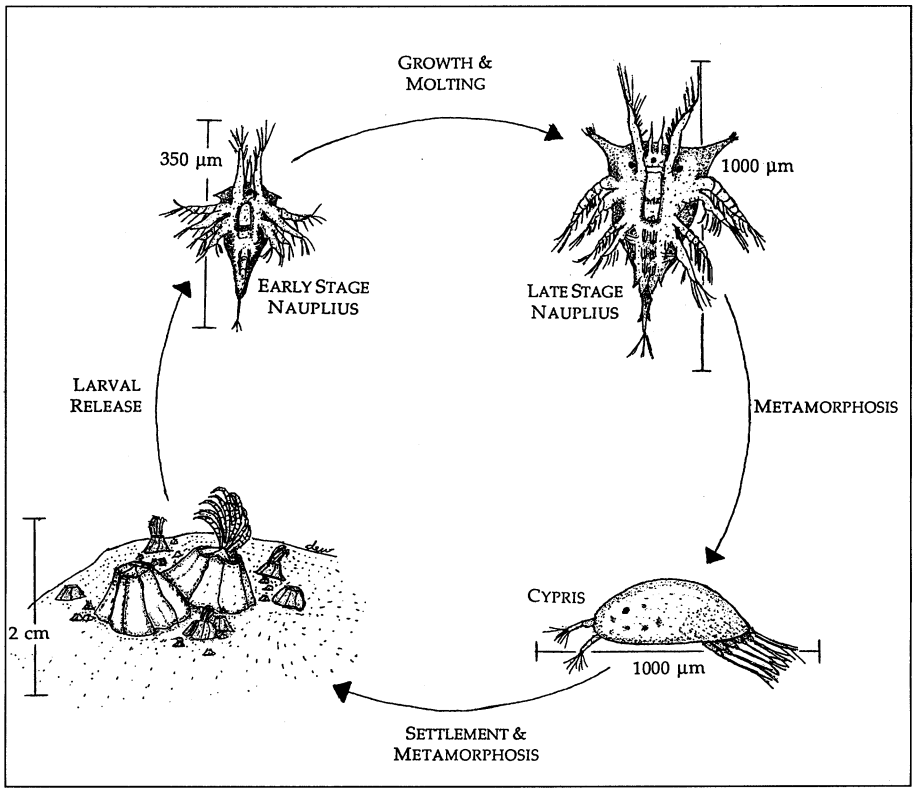

Figure 3. Typical barnacle life cycle. Adults are simultaneous hermaphrodites, and fertilization is internal. After eventual release from the parent, a nonfeeding nauplius larva is followed by five feeding naupliar stages. The sixth stage nauplius metamorphoses to a nonfeeding cyprid larva, which usually metamorphoses to adult form and habitat only after encountering other barnacles of its own species. The thoracic swimming legs of the cyprid become the feeding appendages of the juvenile.

Figure 4. Recruitment of the barnacle *Semibalanus balanoides* at Nahant, Massachusetts. Note the large adults to the left and the many attached cyprids interspersed among the newly metamorphosed individuals. The tendency of cyprid larvae to attach gregariously creates considerable intraspecific competition for space as the barnacles grow.

1991, Pechenik et al. 1993, Wendt 1996). In such cases, the presumed advantages of a prolonged stay in the plankton will not be fully realized.

Fitness costs associated with delayed metamorphosis are especially clear for species that cannot feed as larvae. Barnacles, for example, first develop in the plankton as feeding nauplius larvae but eventually metamorphose to a nonfeeding, terminal larval stage, the cyprid (Figure 3). Cyprids cannot feed in the plankton but must subsist instead on lipids and protein accumulated by the preceding naupliar stages. Cyprids attach to substrata and metamorphose into juvenile barnacles when they encounter specific chemical cues associated with other individuals of their own species (Knight-Jones 1953, Crisp and Meadows 1963, Yule and Walker 1985).

The well-developed tendency of cyprids to attach near other individuals of the same species creates impressive intraspecific competition for space (Figure 4; Connell 1961, Bertness 1989). Delaying cyprid metamorphosis can reduce juvenile competitive ability. *Balanus amphitrite*, for example, can metamorphose within hours of attaining the cyprid stage, but metamorphosis can be prevented for at least 5 days by various means in the laboratory. In experiments conducted by Pechenik et al. (1993), growth rates of newly metamorphosed barnacles were slowed significantly if *B. amphitrite* cyprids were prevented from metamorphosing for as few as 3 days. Such reduced growth rates would compromise the ability of juvenile barnacles to compete for space (Connell 1961) and seriously reduce their likelihood of successfully recruiting to the adult population.

Similar results have been obtained in the laboratory for several bryozoan species (Woollacott et al. 1989, Orellana and Cancino 1991, Wendt 1996). Bryozoans are colonial animals that grow through asexual budding of modular units, called zooids, that remain attached to the parental colony (Figure 5). Competition for space is therefore mediated by rapid increases in zooid numbers, and the competitive advantage should go to colonies that bud the fastest. The microscopic, ciliated larvae (Figure 5) cannot ingest phytoplankton or other particulates. Although the larvae can take up dissolved organic materials from surrounding seawater (Jaeckle 1994), there is as yet no direct evidence that such dissolved materials play a major nutritional role during larval life. Thus, the larvae probably subsist solely on nutrients acquired from the parent during embryogenesis.

In the laboratory, bryozoan larvae metamorphose preferentially in response to certain microbial films on hard surfaces (Brancato and Woollacott 1982). Without those cues, the larvae may continue swimming for at least 10–12 hours; however, they will metamorphose normally during that time if appropriate substrates are introduced to the experimental containers. In experiments conducted with *Bugula stolonifera* (Woollacott et al. 1989), prolonging larval life by as little as 6–8 hours at 20 °C led to significant—and often dramatic—reductions in rates of colony development.

The effects of delayed metamorphosis were similar for *Bugula neritina*: The rate of postmetamorphic development varied inversely with swimming duration (Wendt 1996). Because bryozoans reproduce only after reaching a minimum colony size (e.g., after seven bifurcations in *B. neritina*; Keough 1989), slowing early colony growth should delay the onset of reproduction and decrease long-term reproductive output. Indeed, when young colonies of *B. neritina* were transplanted from the laboratory to the field and examined 14 days later, those established from larvae with long swimming periods (24 hours) had, on average, fewer zooids, fewer bifurcations, and fewer reproductive structures than those established from larvae that were kept swimming for less than 1 hour (Table 1; Wendt in press). Thus, delaying metamorphosis can substantially alter the fitness of bryozoans and barnacles. However, not all species with nonfeeding larvae are equally susceptible to the effects of delayed metamorphosis: Significantly fewer individuals of the polychaete *Capitella* sp. I survived after settlement when metamorphosis was postponed for more than 3 days (at 20 °C), but prolonged swimming did not significantly affect mean juvenile growth rate, time to reproductive maturity, or fecundity of the survivors (Pechenik and Cerulli 1991).

Species with feeding larvae do not generally show reduced fitness when metamorphosis is delayed, although

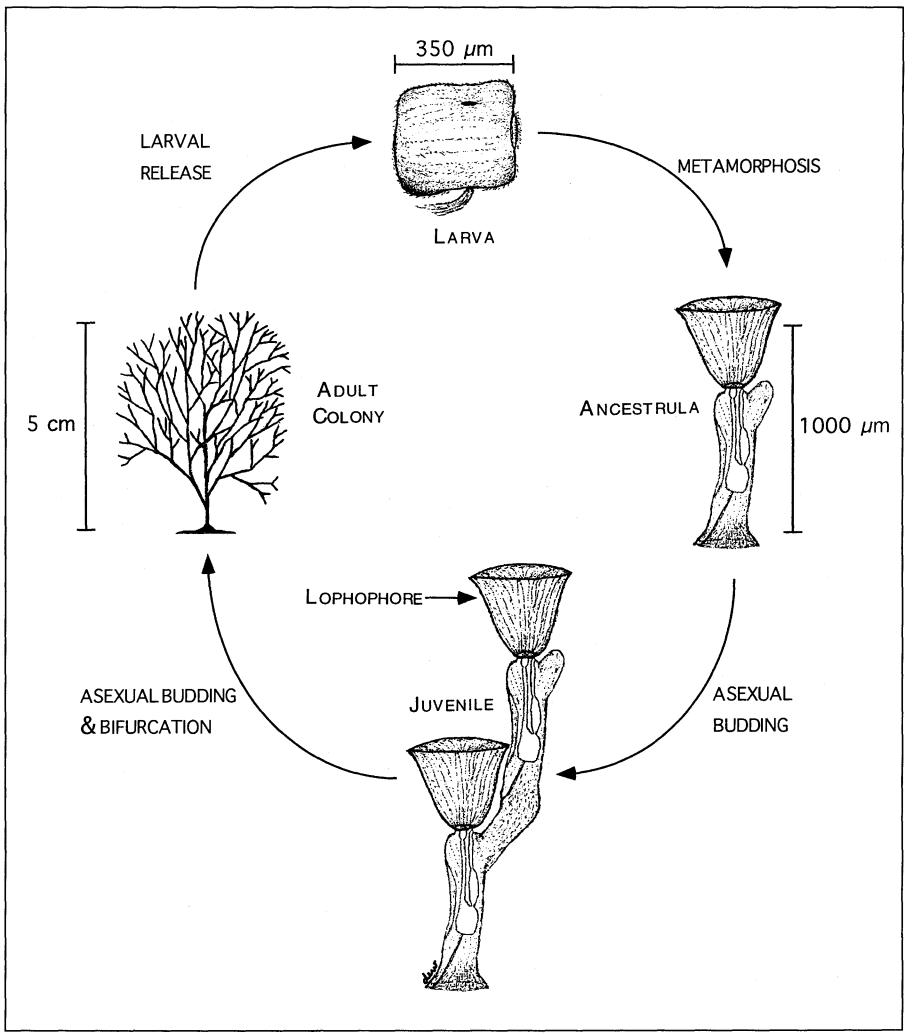

Figure 5. The life cycle of bryozoans in the genus *Bugula*. Each colony is composed of hundreds or thousands of zooids, which release nonfeeding ciliated larvae that are capable of metamorphosing within approximately 2 hours of their release. Each larva attaches and metamorphoses to form a polyp (the ancestrula), which soon begins to feed and to bud off the second member of the colony.

few such species have been studied. Delaying the metamorphosis of *C. fornicata* until larvae metamorphosed spontaneously on clean glassware did not significantly alter juvenile survival, respiration rate, feeding rate, or growth rate (Pechenik and Eyster 1989). Similarly, delaying metamorphosis of the echinoids *Dendraster excentricus* and *Strongylocentrotus droebachiensis* did not significantly increase juvenile mortality or decrease juvenile growth rates, although it may have reduced the tolerance of juvenile *D. excentricus* to physical stress (Highsmith and Emlet 1986). Based on data preserved in the growth rings of otoliths from the tropical reef fishes *Thalassoma bifasciatum* and *Semicossyphus pulcher*, delaying metamorphosis in the field did not significantly reduce juvenile growth rates (Victor 1986, Cowen 1991).

Together, these findings show that delaying metamorphosis, although increasing the likelihood of recruitment into appropriate areas, can clearly carry costs that will potentially reduce fitness, particularly for species that produce nonfeeding larvae. It is equally clear that the consequences of delaying metamorphosis differ substantially among species, both in kind and in magnitude. Species with nonfeeding larvae seem most likely to be affected.

Evidence for reduced fitness effects in the field

To date, relationships between larval experience and postmetamorphic performance have been documented almost entirely in laboratory studies. Victor (1986) and Cowen (1991) found no evidence from field samples that postsettlement growth rates of reef fish are affected by prolonged larval life. However, larval experience may be affecting growth and competitive ability of barnacles in the field. The growth capacity of metamorphosed individuals of the barnacle *Semibalanus balanoides* differed significantly among groups of larvae recruiting on different days at a particular intertidal site in Massachusetts; in general, individuals recruiting later in the season had lower mean growth rates than those recruiting earlier in the season (Figure 6; Jarrett and Pechenik 1997). In those studies, cyprids were allowed to attach to artificial substrata deployed in the field and were then transplanted on those substrata to the laboratory, to be reared at constant temperature and food concentration.

Thus, the documented differences in mean barnacle growth rates can reflect only intrinsic differences in physiological growth capacity of the different cohorts. The results are consistent with the hypotheses that larvae of this species delay their metamorphosis more frequently later in the season, perhaps as suitable habitat fills up with juvenile barnacles, or that they experience substantial reductions in food quality or quan-

Table 1. Mean (± SE) number of zooids, bifurcations, and brood chambers 14 days after metamorphosis in colonies of the bryozoan *Bugula neritina*.[a]

Growth parameters	1 h colony[b]	24 h colony[c]
Zooids	115 ± 7	72 ± 5
Bifurcations	12 ± 0.7	8 ± 0.6
Brood chambers	16 ± 3	3 ± 1

[a]Data from Wendt (in press).
[b]1 h colonies developed from larvae swimming less than 1 hour.
[c]24 h colonies developed from larvae swimming approximately 24 hours before metamorphosis.

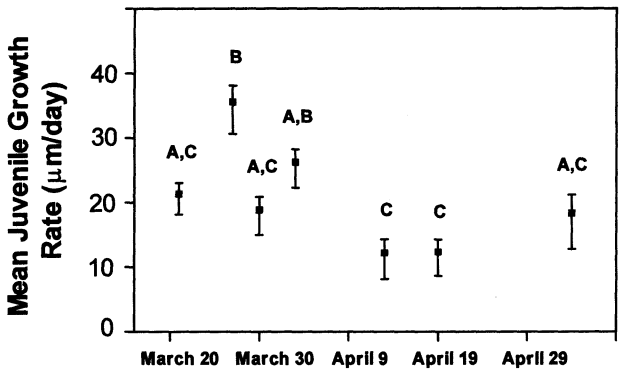

Figure 6. Mean growth rates (± SEM) of young barnacles (*Semibalanus balanoides*) attaching to substrata at Nahant, Massachusetts, on seven different dates in 1995. The larvae are found in the plankton between March and May of each year. For each sampling date, 12 attachment plates were deployed in the field for 24 hours and then returned to the laboratory, where newly attached barnacles were reared under uniform conditions of temperature (16 °C) and food (18 × 10^4 phytoplankton cells/ml) for 7 days. Juvenile growth rates were deduced from changes in basal diameter. Each point represents the mean growth rate of 13–29 animals after adjusting for differences in average attachment size. Identical letters above each bar indicate means that do not differ significantly ($P > 0.05$; GT2 test following analysis of covariance). Data from Jarrett and Pechenik (1997).

tity at different times during the reproductive season.

Mechanisms of action in marine animals

The inverse relationship between larval feeding regime and mean muscle fiber diameter in juvenile reef fish (McCormick and Molony 1992) is easily explained through effects of feeding regime on growth. In most other cases, however, it is not yet clear why the effects of larval experience carry over into juvenile life. Detrimental effects of delayed metamorphosis on juvenile performance in marine invertebrates have so far been documented almost entirely for species with nonfeeding larvae, suggesting that its effects are at least partially mediated by limited energy reserves or nutritional status. Larvae of the gastropod *C. fornicata*, for example, never lose their feeding capability, even during a prolonged extension of time in the plankton (Pechenik 1980). As described earlier, postmetamorphic growth rates were affected for this species only if larvae were starved or given insufficient food for a number of days before metamorphosis (Pechenik 1996a, 1996b).

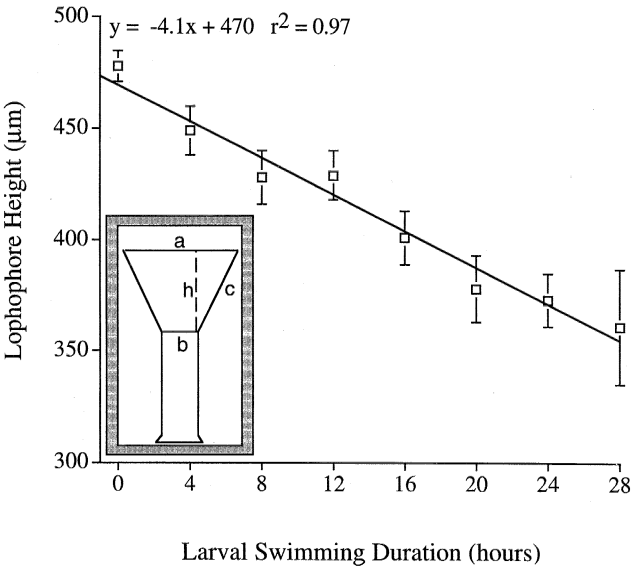

Figure 7. Mean height of the juvenile feeding apparatus (lophophore) as a function of larval swimming duration in the bryozoan *Bugula neritina*. Larvae were sampled every 4 hours and induced to metamorphose by exposing them to 10 mM excess KCl in seawater; elevated concentrations of potassium induce metamorphosis of bryozoan larvae (Wendt and Woollacott 1995). For each juvenile, the top diameter (**a**), bottom diameter (**b**), and tentacle length (**c**) were measured. Based on these measurements, lophophore height was calculated using the equation: Height = $\sqrt{c^2 - (1/4)(a - b)^2}$. Each point is the mean (± SEM) of 8–32 individuals pooled from five replicates. Modified from Wendt (1996).

For species with nonfeeding larvae, there is also some direct evidence that the effects of delayed metamorphosis are caused by overuse of energy reserves during the extended larval swimming period. For the bryozoan *B. neritina*, prolonged larval swimming was associated with significantly reduced size of the juvenile feeding structure, the lophophore: The first juvenile (ancestrula) lophophore was 25% smaller in height (Figure 7) and had 40% less surface area and 50% less volume when larvae were kept swimming for 28 hours at 20 °C than control individuals that were allowed to metamorphose immediately after their release from the parental colony (Wendt 1996). Larvae that had a longer planktonic period probably consumed a larger proportion of their energy reserves while swimming, leaving a smaller proportion available for constructing postmetamorphic feeding structures (Wendt 1996). The reduced mean lophophore sizes probably account for the reduced rates of colony growth described earlier (Woollacott et al. 1989), because food particle collection rates are known to vary with lophophore dimensions in other bryozoan species (Best and Thorpe 1986).

Similarly, the variation in juvenile growth potential documented for the barnacle *Semibalanus balanoides* recruiting in the field may also have a nutritional basis, as suggested by significant fluctuations in the average organic content of newly attached and metamorphosing cyprids during the recruitment season (Jarrett and Pechenik 1997). Cyprid organic content can be influenced by the food conditions experienced by the feeding naupliar stages that precede the nonfeeding cyprid (Figure 3) and by how long the cyprids delay their metamorphosis and remain planktonic.

Nutritional stress is a major cause of the temporal variation in cyprid organic content (Jeremiah Jarrett, unpublished data). Stage VI nauplii were removed from plankton samples taken on six dates in 1996 and maintained at field temperature (4–6 °C) in filtered seawater. The organic content of each individual metamorphosing to the cyprid stage during the next 16 hours was then measured. The organic content of these newly

metamorphosed cyprids differed significantly among samples collected on different dates, generally being lower later in the spring (Figure 8), which supports the hypothesis that cyprid energy content is determined largely by the nutritional status of the preceding naupliar stages of development.

However, variation in cyprid energy content does not always predict juvenile growth rate. For example, the mean energy content of individuals attaching to substrates in the field on 20 March 1995 did not differ significantly ($P > 0.05$) from that of individuals attaching on 27 March (Jarrett and Pechenik 1997), even though juvenile growth rates did differ significantly for individuals recruiting on those dates ($P < 0.05$; Figure 6). Also, delaying metamorphosis of the spionid polychaete *Polydora ligni* reduced juvenile growth rates and adult fecundity, even when larvae were fed on natural phytoplankton assemblages (Qian et al. 1990). Conversely, delaying metamorphosis of the polychaete *Capitella* sp. I had no significant effect on mean juvenile growth rate, time to reproductive maturity, or fecundity, as discussed earlier, even though the larvae are nonfeeding (Pechenik and Cerulli 1991). These findings suggest that the causes of variation in juvenile performance may sometimes be more complex than simple variation in larval energy content. Perhaps some gene products transcribed early in development are needed for proper organogenesis or physiological function following metamorphosis; some stresses might interfere with either the timing or the magnitude of transcriptional or translational processes in some species.

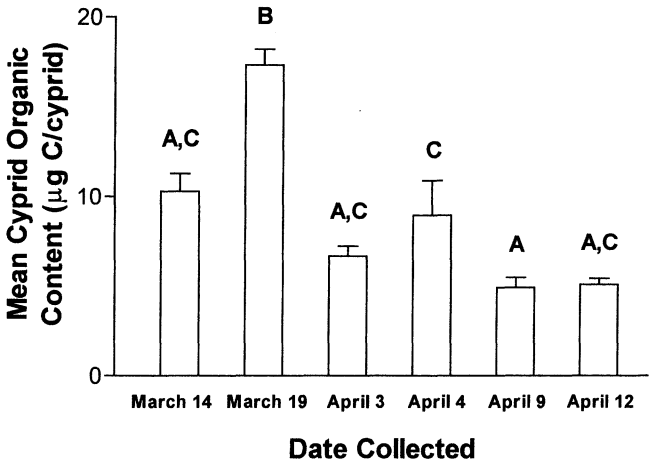

Figure 8. Mean organic content of barnacles (*Semibalanus balanoides*) metamorphosing from stage VI nauplii to cyprids within 16 hours after their collection from the plankton near Nahant, Massachusetts, on 6 days during 1996. Larvae of this species are found in the plankton between March and May of each year. Different letters above each bar indicate significantly different means ($P < 0.05$). Because all individuals were collected as nauplii and metamorphosed in the laboratory soon after being collected, differences in mean cyprid organic content must reflect differences in the nutritional condition of nauplii at the time of collection rather than differences in the lengths of time that individuals were in the cyprid stage. Each bar (+ SEM) indicates the mean of measurements made on 6–14 individual cyprids (except March 14 data, which indicates the mean of measurements made on 2 cyprids).

Examples from other groups

There is good reason to think that embryonic or larval experiences commonly influence juvenile performance in amphibians, fishes, and insects, although documentation is surprisingly rare. Among amphibians, declines in food availability commonly precipitate metamorphosis at smaller than average sizes (Travis 1984, Alford and Harris 1988, Semlitsch et al. 1988, Newman 1992, Audo et al. 1995). Size at metamorphosis can have important repercussions in later life, although the effects have been documented in only a few studies to date. In the salamander *Ambystoma talpoideum*, for example, smaller size at metamorphosis was associated with both smaller size and greater age at first reproduction (Semlitsch et al. 1988). Similarly, smaller body size at metamorphosis correlated with longer time to reach reproductive maturity, smaller body size at reproductive maturity, and reduced fecundity in the woodfrog, *Rana sylvatica* (Berven 1990). Larval feeding history can clearly influence lifetime fitness of amphibians, even when juvenile survival is not affected (Semlitsch et al. 1988).

Different sorts of effects of food stress on lifetime fitness have been suggested but not yet documented for several coral reef fish species. Fish larvae recruiting to reefs at different times can differ dramatically in average biochemical composition (Kerrigan 1996), suggesting varied nutritional experiences of larvae in the field. Recent laboratory studies by McCormick and Molony (1992) demonstrate that reduced food supply to larvae can decrease the average size at settlement, average diameter of muscle fibers, and average feeding rates in juvenile goatfish, *Upenaeus tragula*. Although differences in size and biochemical composition at settlement do not necessarily alter the susceptibility of juvenile fish to predators (McCormick and Kerrigan 1996), other properties, such as juvenile growth rates, ability to compete successfully for food and mates, and time to sexual maturity, might be affected (Kerrigan 1996, McCormick and Kerrigan 1996).

Negative effects of larval experience on juvenile or adult performance have been reported for some insect species. In the flesh fly, *Sarcophago bullata*, prolonging larval diapause in the laboratory reduced fertilization success (Denlinger 1981). By crossing males that had experienced prolonged diapause as larvae with females that had not, and vice versa, Denlinger (1981) showed that prolonging diapause affected only female reproductive fitness. Similarly, prolonged diapause of the bruchid *Kytorhinus sharpianus* significantly reduced the average number of eggs deposited, in part by increasing the proportion of females that deposited no eggs at all (Ishihara and Shimade 1995). We have not encountered comparable studies for other insect species.

These findings thus indicate that the influence of larval experience on postmetamorphic fitness is not limited to marine invertebrates. Instead, it seems to be widespread among species with complex life cycles.

Future work

Metamorphosis does not necessarily signal a completely new beginning within the life cycles of marine invertebrates. Certain larval experiences—even short-term ones—can clearly carry over to future stages of development. The phenomenon is known mostly from laboratory studies, although even in these cases the range of examples is limited. Additional studies need to be conducted using a wider range of species, including insects, amphibians, and fishes. Such studies should consider a wider range of stresses and examine a wider range of responses, looking for effects of embryonic and larval experience on juvenile survival, age at maturity, growth rate, mating behavior, fecundity, and competitive ability. The literature reviewed in this article suggests that nutritional and other experiences during early development are likely to reduce juvenile performance in a variety of ways in a wide range of species across most animal groups, and perhaps in plants as well. How the effects of larval experience on postmetamorphic fitness are mediated, and whether those effects are mediated by similar mechanisms in different species, remain to be determined.

The potential for embryonic and larval experiences to reduce juvenile or adult fitness has broad implications in a wide range of areas. For example, many marine invertebrate and fish populations show great variation in size from year to year; this variation is often related to changes in larval mortality and in the numbers of larvae supplied to particular areas in different years (Thorson 1950, Bailey and Houde 1989, Hill 1991, Shanks 1995) and in the extent of postmetamorphic mortality (Gosselin and Qian 1997, Hunt and Scheibling 1997). The role of larval experience in increasing the extent of postmetamorphic mortality in the field—through reduced ability to compete for food or space, for example—has yet to be examined.

Early experience may also affect sensitivity to environmental contaminants. Embryonic and larval stages are typically far more sensitive to thermal, salinity, and pollutant stresses than are juvenile and adult stages of the same species (e.g., Calabrese et al. 1973, Moore and Dwyer 1974). However, studies of embryonic and larval tolerance to environmental stresses have generally ended at or before metamorphosis. Because short-term food deprivation and delayed metamorphosis in the larval stage can clearly affect juvenile and adult fitness, we predict that exposing larvae to sublethal pollutant concentrations and other environmental stresses will also affect postmetamorphic development in many species; fitness effects will probably be found when they are looked for.

Early life stresses may also influence the likelihood of successful invasion by marine species transported in ship ballast water. During their days or weeks of transport in ship ballast water (Ruiz et al. 1997), larvae are likely to be both delaying their metamorphosis and experiencing nutritional stress; species that are least sensitive to such stresses may be the most likely to invade successfully following their discharge and metamorphosis.

Reductions in juvenile fitness due to delayed metamorphosis or temporary nutritional stress also have implications for the aquaculture industry. Juvenile growth rates of cultured clams and oysters, for example, might suffer substantially if larvae are allowed to delay their metamorphosis for too long after becoming competent, or if larvae experience nutritional stress during critical periods before metamorphosis.

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