Metamorphosis Is Not a New Beginning

Larval experience influences juvenile performance

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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.”

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
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 1993) 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 1993, Morgan 1995), few studies have considered that food limitation experienced dur-

![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.](image-url)
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 fornicate; 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. fornicate 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 at 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...
Species with feeding larvae do not generally show reduced fitness when metamorphosis is delayed, although
reef fish are affected by prolonged
larval experience and postmetamorphic
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almost entirely in laboratory stud­

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a particular intertidal site in Massa­
chusetts; in general, individuals re­
cruiting later in the season had lower
mean growth rates than those re­
cruiting earlier in the season (Figure 6;
Jarrett and Pechenik 1997).

Thus, the documented differences
among species, both in kind and in magnitude. Speci­
cies with nonfeeding larvae seem
most likely to be affected.

Evidence for reduced fitness
effects in the field

To date, relationships between lar­
val experience and postmetamorphic
performance have been documented
almost entirely in laboratory stud­
found no evidence from field samples
that postsettlement growth rates of
reef fish are affected by prolonged
larval life. However, larval experi­
ence may be affecting growth and
competitive ability of barnacles in
the field. The growth capacity of
metamorphosed individuals of the
barnacle Semibalanus balanoides dif­
fered significantly among groups of
larvae recruiting on different days at
a particular intertidal site in Massa­
chusetts; in general, individuals re­
cruiting later in the season had lower
mean growth rates than those re­
cruiting earlier in the season (Figure 6;
Jarrett and Pechenik 1997). In those
studies, cyprids were allowed to at­
tach 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 lar­
vae of this species delay their meta­
morphosis more frequently later in
the season, perhaps as suitable habi­
tat 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.4

<table>
<thead>
<tr>
<th>Growth parameters</th>
<th>1 h colony*</th>
<th>24 h colony*</th>
</tr>
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<tbody>
<tr>
<td>Zooids</td>
<td>115 ± 7</td>
<td>72 ± 5</td>
</tr>
<tr>
<td>Bifurcations</td>
<td>12 ± 0.7</td>
<td>8 ± 0.6</td>
</tr>
<tr>
<td>Brood chambers</td>
<td>16 ± 3</td>
<td>3 ± 1</td>
</tr>
</tbody>
</table>

*Data from Wendt (in press).
*1 h colonies developed from larvae swimming less than 1 hour.
*24 h colonies developed from larvae swimming approximately 24 hours before metamorphosis.
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. formicata, 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).

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.

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, Upeneus 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 cross-mating 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 Shimada 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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