

Larval experience and latent effects—metamorphosis is not a new beginning

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Synopsis For many years ecologists have documented the remarkable within-species variation inherent in natural systems—for example, variability in juvenile growth rates, mortality rates, fecundities, time to reproductive maturity, the outcomes of competitive interactions, and tolerance to pollutants. Over the past 20 years, it has become increasingly apparent that at least some of this variation may reflect differences in embryonic or larval experiences. Such experiences may include delayed metamorphosis, short term starvation, short term salinity stress, or exposure to sublethal concentrations of pollutants or sublethal levels of ultra violet irradiation. Latent effects—effects that have their origins in early development but that are first exhibited in juveniles or adults—have now been documented among gastropods, bivalves, echinoderms, polychaetes, crustaceans, bryozoans, urochordates, and vertebrates. The extent to which latent effects alter ecological outcomes in natural populations in the field, and the mechanisms through which they are mediated are largely unexplored.

“The concept that events in early life could play a major role in determining health in later life may be intuitively difficult to accept initially.” (Desai and Hales 1997)

Introduction

Metamorphosis is a time of great revolution—commonly it is a dramatic transition to a new life in a new place in a new body. But it has long acted as an artificial barrier in marine research: larval biologists have traditionally ended their studies at metamorphosis, and benthic ecologists have typically begun their studies after metamorphosis has been completed, often long after it has been completed. In the marine literature at least, it has not been common to see larvae and juveniles of the same species included in the same study.

But over the past 20 years or so it has become increasingly apparent that at least some of the things experienced by marine embryos and larvae can influence events after metamorphosis has taken place. Here, I summarize what is known about those effects for marine invertebrates and provide what seem to be examples of similar phenomena for some vertebrates and terrestrial insects. It seems that research on marine invertebrates, amphibians, and mammals has independently converged on this same issue: experiences that

occur early in development may first reveal themselves at later stages of development.

My interest in exploring the relationship between larval experience and postmetamorphic performance began with an interest in the ability of marine invertebrate larvae to delay their metamorphosis, and why that ability to delay varied so much among and within species (Pechenik 1980). I first suggested that delaying metamorphosis might have fitness costs for benthic juveniles in 1985. My reasoning was that the phenomenon of “spontaneous metamorphosis,” in which lab-reared larvae eventually metamorphosed despite our best efforts to prevent it, made little sense unless juvenile or adult fitness declined once larvae postponed their metamorphosis beyond a certain age (Pechenik 1985; see also Pechenik and Eyster 1989). But the first evidence for this phenomenon seems to have been published by Claus Nielsen 4 years earlier, in 1981, for the bryozoan “*Hippodiplosia insculpta*.” Although the findings were not quantified, Nielsen (1981, p 106) noted that “The majority of larvae which were allowed to settle within the first 6 hours after liberation developed into ancestrulae with protruding lophophores within about three days. Larvae which settled after a longer free life often developed slowly and into unusually small ancestrulae which in most cases died without having protruded the lophophores...”. In the past 25 years, detrimental

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effects of delaying metamorphosis have been demonstrated for a number of different species in a number of different phyla, and the range of embryonic and larval experiences that influence postmetamorphic success has been broadened to include nutritional stress, salinity stress, exposure to UV-irradiation, and exposure to sublethal concentrations of pollutants (Table 1). Clearly, metamorphosis is not necessarily a new beginning (Pechenik and others 1998).

Definitions

The kinds of effects I will be discussing in this article have recently come to be called “carryover effects” in the ecological literature (for example, Goater 1994; Pahkala and others 2001; Phillips 2002, 2004; Altwegg and Reyer 2003; Marshall and others 2003; Ng and Keough 2003). This term is commonly used in the medical literature, in the context of determining whether the beneficial effects of a particular treatment “carry over” for a time after the treatment ends (for example, Baker 2004; Crust 2004; Murray and others 2004). But that descriptor often does not fit the situation described in this review: although the effects discussed here do originate in embryonic and larval experiences, they are expressed only in juveniles or adults. Thus, these are not characteristics that simply “carry over” from early development into juvenile life or adulthood. Rather, they involve characteristics that originate in embryonic and larval experiences but become visible only in juvenile or adult stages. In this article I will refer to them as “latent effects.” “Latent effects,” as I will use the term, do not include the effects of adult conditioning on offspring quality (for example, Bayne and others 1975; McCormick 1998)—those effects already have a perfectly good name: “maternal effects” (for example, Bayne and others 1975; Mousseau and Dingle 1991; Fox and others 1995; McCormick 1998; Agrawal and others 1999).

Types of treatments producing latent effects

Delayed metamorphosis

Marine invertebrates typically become metamorphically competent at a certain point in development, meaning that they become responsive to certain external cues that can trigger metamorphosis into habitats appropriate for juvenile growth and survival (reviewed by Pechenik 1990); in the absence of those cues, the larval state is prolonged, potentially for very long periods in some species (reviewed by Pechenik 1990). In the laboratory, the larvae of at least some

species eventually metamorphose without any such cues being provided; that is, they metamorphose “spontaneously” (Pechenik 1984; Pechenik 1985; Highsmith and Emlet 1986; Gaudette and others 2001; Pechenik, Li, and others 2002). Although this ability to prolong larval life in the absence of appropriate environmental signals is usually viewed favorably (reviewed by Pechenik 1990, 1999), even very short delay periods can sometimes lead to serious fitness declines in juveniles and adults—in particular, decreased survival and reduced rates of postmetamorphic growth or development.

Latent effects resulting from delayed metamorphosis have now been documented and quantified for a number of species in a variety of groups (Table 1). For example, when larvae of some species [for example, the bryozoan *Bugula stolonifera* (Woollacott and others 1989) and the colonial seasquirt *Diplosoma listerianum* (Marshall and others 2003)] were made to delay metamorphosis by 2–10 h, the rates at which colonies developed after metamorphosis were slowed significantly, and often dramatically. Similarly, prolonging larval life for barnacle cyprids (*Balanus amphitrite*) by only 3 days resulted in dramatically reduced rates of juvenile growth (Pechenik and others 1993).

Such latent effects can persist for at least several weeks. For example, Wendt (1998) delayed the metamorphosis of *Bugula neritina* larvae for 24 h and then transplanted the colonies into the field and observed them for 2 weeks. Colonies derived from long-swimming larvae accumulated autozooids at a significantly slower rate than did control colonies, and took longer to become reproductively mature. Of particular importance, the experimental colonies in Wendt’s study had many fewer brood chambers at the end of the 2 week field deployment and were accumulating brood chambers at a slower rate than control colonies, suggesting that colony fecundity was permanently reduced by the additional larval swimming time. Similarly, preventing metamorphosis for just 2–3 h resulted in significantly smaller zooid sizes for the colonial ascidian *D. listerianum*, and, as indicated by measurements of branchial basket dimensions, those smaller sizes were still in evidence for zooids forming 3 weeks after colonies had been transplanted into the field (Marshall and others 2003).

Other evidence for latent effects of delayed metamorphosis in marine invertebrates includes reduced juvenile survival and growth rates in a decapod crustacean (Gebauer and others 1999), reduced post-settlement survival or reduced growth for some polychaetes and sea urchins (Highsmith and Emlet 1986; Qian and others 1990; Pechenik and Cerulli 1991; Qian and Pechenik 1998; Vätilingon and others

Table 1 Studies of latent effects in animals

Taxon	Species	Treatment in larval or embryonic stage	Latent effects?	References
Sponges	<i>Sigmadocia caerulea</i>	Swimming duration	Yes	Maldonado and Young (1999)
Bryozoans	<i>'Hippodiplosia' insculpta</i>	Delayed metamorphosis	Yes	Nielsen (1981)
	<i>Bugula stolonifera</i>	Delayed metamorphosis	Yes	Woollacott and colleagues (1989)
	<i>Bugula neritina</i>	Delayed metamorphosis	Yes	Wendt (1998)
	<i>Celleporella hyalina</i>	Delayed metamorphosis	Yes	Orellana and Cancino (1991)
	<i>Watersipora subtorquata</i>	Copper	Yes	Ng and Keough (2003)
Gastropods	<i>Crepidula fornicata</i>	Delayed metamorphosis	No	Pechenik and Eyster (1989)
	<i>C. fornicata</i>	Low food concentration	Yes	Pechenik, Estrella, and colleagues (1996); Pechenik, Hammer, and colleagues (1996); Pechenik, Jarrett, and colleagues (2002)
	<i>C. fornicata</i>	Cadmium	No	Pechenik and colleagues (2001)
	<i>Phestilla sibogae</i>	Delayed metamorphosis with fed larvae	No	Miller and Hadfield (1990)
	<i>P. sibogae</i>	Delayed metamorphosis with starved larvae	Yes	Miller (1993)
Bivalves	<i>Dreissena polymorpha</i>	Food quality	Yes	Wacker and von Elert (2002)
	<i>Mytilus galloprovincialis</i>	Low food concentration	Yes	Phillips (2002)
Polychaetes	<i>Polydora ligni</i>	Delayed metamorphosis	Yes	Qian and colleagues (1990)
	<i>Capitella</i> sp. I	Low salinity	Yes	Pechenik and colleagues (2001)
	<i>Capitella</i> sp. I	Cadmium	No	Pechenik and colleagues (2001)
	<i>Hydroides elegans</i>	Delayed metamorphosis; Starvation	Yes	Qian and Pechenik (1998)
Crustaceans	<i>Chasmagnathus granulata</i>	Delayed metamorphosis	Yes	Gebauer and colleagues (1999)
	<i>Balanus amphitrite</i>	Delayed metamorphosis	Yes	Pechenik and colleagues (1993)
	<i>B. amphitrite</i>	Low food concentration	Yes	Thiyagarajan and colleagues (2003)
	<i>Balanus glandula</i>	Low food concentration	Yes	Emler and Sadro (2005)
Insects	<i>Ondotocerus albicorne</i>	Increased silk usage	Yes	Stevens and colleagues (1999)
	<i>Kytorhinus sharpianus</i>	Prolonged diapause	Yes	Ishihara and Shimada (1995)
Echinoids	<i>Dendraster excentricus</i>	Delayed metamorphosis	Yes ^a	Highsmith and Emler (1986)
	<i>Echinarachnius parma</i>	Delayed metamorphosis	Yes ^a	Highsmith and Emler (1986)
	<i>Paracentrotus lividus</i>	Delayed metamorphosis	Yes ^a	Vařtilingon and colleagues (2001)
	<i>Strongylocentrotus franciscanus</i> and <i>Strongylocentrotus purpuratus</i>	Food concentration	Yes	Miller and Emler (1999)
Urochordates	<i>Diplosoma listerianum</i>	Larval swimming vigor	Yes	Marshall and colleagues (2003)
	<i>Styela plicata</i>	Delayed metamorphosis	No	Thiyagarajan and Qian (2003)
Fish	<i>Oncorhynchus gorbuscha</i>	Crude oil	Yes	Heintz and colleagues (2000)
	<i>Upeneus tragula</i>	Food availability	Yes	McCormick and Molony (1992)
Amphibians	<i>Ambystoma opacum</i>	Larval density	Yes	Scott (1994)
	<i>Ambystoma talpoideum</i>	Delayed metamorphosis	Yes	Semlitsch and colleagues (1988)
	<i>Bufo bufo</i>	Larval density	Yes	Goater (1994)
	<i>Hyla versicolor</i>	Larval competition	Yes	Relyea and Hoverman (2003)
	<i>Rana sylvatica</i>	Predators	Yes	Relyea (2001)
	<i>Rana temporaria</i>	UV-irradiation	Yes	Pahkala and colleagues (2001)
	<i>Rana lessonae</i> and <i>Rana easculenta</i>	Larval density	Yes	Altwegg and Reyer (2003)
Turtles	<i>Chelydra serpentina</i>	Water availability	Yes	Miller and colleagues (1987)
Birds	<i>Parus caeruleus</i>	Nutritional stress	Yes	Merilä and Svensson (1997)
Mammals	<i>Homo sapiens</i>	Nutritional stress <i>in utero</i>	Yes	Ravelli and colleagues (1976)
	<i>H. sapiens</i>	Nutritional stress <i>in utero</i>	Yes	Desai and Hales (1997)
	<i>H. sapiens</i>	Nutritional stress <i>in utero</i>	Yes	Barker (1995)

^aResults ambiguous due to high postmetamorphic mortality.

2001), and reduced reproductive potential for a spionid polychaete (Qian and others 1990) (Table 1).

However, delaying metamorphosis does not always alter juvenile or adult fitness. Planktotrophic larvae of the marine gastropod *Crepidula fornicata*, for example, typically become competent to metamorphose after about 7–11 days at 23–25°C (Pechenik and Gee 1993; Pechenik, Estrella, and others 1996; Pechenik, Hammer, and others 1996), and can then retain the larval form for about another 10–16 days in the absence of appropriate environmental cues (Pechenik 1984; Pechenik and Lima 1984). Eventually these larvae metamorphose “spontaneously,” that is, despite our best efforts to prevent it in the laboratory (Pechenik 1985; Pechenik, Li, and others 2002). Larvae that metamorphosed spontaneously, after the longest possible delay period at that rearing temperature, gave rise to juveniles that did not differ from control individuals metamorphosing earlier either in mean survival, growth rate, respiration rate, or feeding rate (Pechenik and Eyster 1989). Delaying metamorphosis similarly had no significant effect on juvenile tolerance to high temperatures or low salinities (Pechenik and Eyster 1989). Similarly, delaying metamorphosis of the solitary ascidian *Styela plicata* for up to 48 h (at 10°C) did not alter postmetamorphic survival or rate of morphological development (Thiyagarajan and Qian 2003), even though that species has lecithotrophic, nonfeeding larvae. Miller and Hadfield (1990) reported that delaying metamorphosis of the nudibranch gastropod *Phestilla sibogae* for up to 28 days had no effect on juvenile survival, mean adult body weight, adult fecundity, or adult lifespan, as long as larvae were well fed while metamorphosis was delayed (Miller and Hadfield 1990; Miller 1993). Although delaying metamorphosis of the polychaete *Capitella* sp. I for 3–4 days at 20°C reduced postsettlement survival substantially (Pechenik and Cerulli 1991), delaying metamorphosis of this same species for 5 days at 15°C did not (Butman and others 1988).

Although the larvae of at least some tropical reef fish can also delay their metamorphosis (Victor 1986; Cowen 1991; Jenkins and May 1994; McCormick 1999), there is no direct evidence for any effect of prolonged larval life on subsequent juvenile or adult fitness (Victor 1986; Cowen 1991). There is, however, evidence that juvenile survival is directly related to larval growth rates (Shima and Findlay 2002) and to larval physiological condition at settlement (Searcy and Sponaugle 2001), which can differ dramatically among individuals and over time (McCormick and Molony 1993; Kerrigan 1996); thus, to the extent that delaying metamorphosis affects larval growth rates or physiological condition at settlement, delaying

metamorphosis may have latent effects in some fish species as well.

In a different sense, amphibians can also delay their metamorphosis: in particular, the timing of metamorphosis is affected by overcrowding (Goater 1994; Scott 1994; Relyea and Hoverman 2003; reviewed by Newman 1992) and the presence or absence of predatory dragonfly larvae (reviewed by Newman 1992; Relyea 2001; Van Buskirk and Saxer 2001; Altwegg and Reyer 2003). This situation differs from that already described for marine invertebrates in that there is no indication that tadpole larvae metamorphosing later than average were physiologically capable of metamorphosing any earlier (discussed by Pechenik 2001), so this is delayed metamorphosis only in the sense that the animals metamorphosed at a later date. In any event, tadpole larvae that metamorphosed later than average tended to show lower postmetamorphic survival in the field, lower postmetamorphic growth rates, and smaller mean adult size—a likely indicator of reduced reproductive potential (for example, Semlitsch and others 1988; Altwegg and Reyer 2003).

Although insect larvae also do not delay their metamorphosis per se, prolonged diapause has resulted in diminished reproductive potential in several species (Denlinger 1981; Ishihara and Shimada 1995).

Food limitation and nutritional stress

Larvae of the nudibranch *P. sibogae* are facultative planktotrophs and thus can develop through metamorphosis without food (Miller 1993). However, rearing larvae in filtered seawater resulted in lower mean juvenile weight, decreased juvenile survival, decreased weight at reproductive maturity, and longer mean time to reproductive maturity (Miller 1993); mean adult survival and longevity, however, were not affected by food deprivation during larval development (Miller 1993).

Depriving competent larvae of *C. fornicata* of food for 2–5 days had the unanticipated effects of stimulating metamorphosis (Pechenik, Estrella, and others 1996) and depressing rates of juvenile growth in the presence of excess food (Pechenik, Estrella, and others 1996, Pechenik, Hammer, and others 1996). Reduced growth rates for juveniles of *C. fornicata* were documented even when the larvae were food limited for only 48 h very early in development and then returned to abundant food; although larval growth rates were initially depressed after starved larvae were given food again, larval growth rates returned to control levels long before metamorphosis was induced (Pechenik and others 1998; Pechenik, Jarrett, and others 2002). Thus, latent effects on juvenile growth were seen even

though the larvae had apparently fully recovered from the stress. Similarly depressive effects on juvenile growth rates were seen for *C. fornicata* even if food concentrations were simply reduced for 2–3 days (1×10^3 cells/ml rather than 18×10^4 cells/ml—Pechenik, Estrella, and others 1996). In both cases, however, juvenile growth rates returned to control levels within a week after metamorphosis in several experiments (Pechenik, Jarrett, and others 2002), suggesting that the latent effects of food limitation during larval development are temporary in this species. Similarly, initially reduced growth of juvenile barnacles (*B. amphitrite*) eventually returned to control levels in the presence of abundant food, but only after 1 to several weeks (Thiyagarajan and others 2003; Emler and Sadro 2006); in those studies, treated nauplii were reared at lower than normal food concentrations before their metamorphosis to the cyprid stage.

Among echinoderms, latent effects have been looked for only among echinoids (Highsmith and Emler 1986; Miller and Emler 1999; Väitilingon and others 2001). Although some of the data are ambiguous due to very high postmetamorphic mortality, rearing larvae of the echinoid *Strongylocentrotus purpuratus* at half the normal food concentration clearly resulted in depressed growth rates for well-fed juveniles (Miller and Emler 1999). Similarly Phillips (2002, 2004) found latent effects following nutritional limitation during larval development for the mussel *Mytilus galloprovincialis*, both in laboratory culture and in field transplants; both juvenile growth rates and the proportion of juveniles recovered at the end of the study (likely reflecting juvenile mortality) were reduced for individuals that had been nutritionally stressed as larvae. Latent effects of nutritional limitation during larval development have also been reported for the freshwater bivalve *Dreissena polymorpha* (Wacker and von Elert 2002) and the polychaetes *Capitella* sp. I and *Polydora ligni* (Qian and others 1990). For the terrestrial armyworm *Pseudaletia separata*, males produced larger spermatophores if they were reared under crowded conditions as larvae (He and Miyata 1997).

Among vertebrates, nutritional deprivation during early development has been shown to affect growth and muscle development in the goatfish *Upeneus tragula* (McCormick and Molony 1992); survival and reproductive success in many bird species (reviewed by Merilä and Svensson 1997); and the incidence of obesity, adult onset diabetes, coronary heart disease, abnormal liver function, and reduced birth weight in humans (Ravelli and others 1976; Desai and Hales 1997; Barker 1995). For example, during WWII, the German occupation cut off supply lines to the western

Netherlands for 6 months, so that pregnant women living in that region experienced “nutritional stress” for a very well-defined period of time during their pregnancies (Ravelli and others 1976; Desai and Hales 1997). Then the supply lines were reopened and food started flowing again, so we know very precisely when the nutritional stress began and ended. Many years later, it turns out, the sons of women who suffered the famine in the first half of pregnancy were much more likely to be obese as adults, and the daughters of women (but not the women themselves) who experienced the famine during the first two trimesters of pregnancy had an increased likelihood of birthing babies of below normal weight (Ravelli and others 1976; Desai and Hales 1997).

Salinity stress

The deposit-feeding polychaete *Capitella* sp. I showed latent effects in response to osmotic stress (Pechenik and others 2001). Maintaining larvae at 10–12 ppt salinity for 24–48 h resulted in decreased postmetamorphic survival and reduced growth rate, even though no larvae died during exposure.

Increased energy expenditure

The tadpole larvae of seasquirts are lecithotrophic (yolk-feeding) and often show a pronounced shadow response: that is, in response to a shadow they swim frantically, as though trying to escape a potential predator. When larvae of the colonial seasquirt *D. listerianum* were forced to swim frantically for 3 h, by repeatedly switching on and off ambient lighting, and then allowed to metamorphose, rates of colony development were significantly depressed, and to a much higher degree than when metamorphosis was delayed under constant lighting (Marshall and others 2003). Similarly, when the protective houses of caddis fly larvae (*Odontocerum albicorne*) were repeatedly destroyed, forcing the larvae to continually rebuild their houses, the larvae metamorphosed into adults with smaller than normal wings and lighter thoraces, probably because of increased expenditure of protein in silk formation during development (Stevens and others 1999).

Pollution

I am aware of only 3 studies on the ability of sublethal pollution exposure to produce latent effects in aquatic animals. In one study, the larvae of the gastropod *C. fornicata* were exposed to concentrations of cadmium in seawater up to a nominal concentration of 20,000 $\mu\text{g/l}$ (Pechenik and others 2001) for 48 h. Although many larvae died at concentrations of

2500 $\mu\text{g/l}$ or higher, some larvae survived at concentrations of up to 10,000 $\mu\text{g/l}$. The surviving larvae were then reared in uncontaminated seawater for another 8 days and induced to metamorphose. Juveniles were then reared for 5 days with excess phytoplankton in control seawater. Remarkably, cadmium exposure produced no measurable latent effects: neither juvenile survival nor juvenile growth rates were significantly affected by exposure to cadmium as larvae (Pechenik and others 2001). Similar findings were reported for the polychaete *Capitella* sp. I; although the reported LD-50 for this species is about 750 $\mu\text{g/l}$ (Reish and others 1976), exposing larvae to concentrations as high as 2000 $\mu\text{g/l}$ for up to 48 h had no effect on postsettlement survival or fecundity, and probably had no effect on juvenile growth (Pechenik and others 2001).

Ng and Keough (2003) exposed larvae of the encrusting bryozoan *Watersipora subtorquata* to a sublethal concentration of copper (100 $\mu\text{g/l}$) for 6 h and then induced larvae to metamorphose. The young colonies were then transplanted into the field. In winter transplants, colonies survived well for 11 weeks regardless of whether larvae had been exposed to copper or not; thereafter, however, colony survival declined substantially, and the decline was significantly greater if larvae had been exposed to copper for 6 h. Thus, latent effects were observed, but not until 12–14 weeks after colonies were transferred to the field! Similar latent effects of copper exposure on colony survival were seen in summer transplants (Ng and Keough 2003). Exposing larvae to copper also reduced rates of colony growth (Ng and Keough 2003).

Exposing embryos of pink salmon (*Oncorhynchus gorbuscha*) to sublethal concentrations of crude oil (5.4 ppb) apparently reduced the survival of juveniles released into the field, and exposing embryos to concentrations as low as 18 ppb reduced juvenile growth rates in the laboratory (Heintz and others 2000).

UV-irradiation

UV-irradiation of embryos produced latent effects in an amphibian. Fertilized eggs of *Rana temporaria* were protected from exposure to UV-B irradiation or exposed to 2 levels of irradiation until hatching (Pahkala and others 2001). All larvae were then reared without exposure to UV-B. Although the researchers found no effects of UV-B exposure on embryonic survival, time to hatching, size at hatching, or frequency of developmental abnormalities at hatching, they did report a significant effect many weeks later on time to metamorphosis (mean larval period was

lengthened), weight at metamorphosis (mean body weight was reduced), and incidence of developmental abnormalities (incidence was increased).

Variation in response within and among species

Not all species respond to the same pre-metamorphic stresses in the same way, and different stresses have different effects within species. For example, in the polychaete *Capitella* sp. I, delaying metamorphosis by more than 3 days at 20°C decreased postsettlement survival significantly but had no apparent effect on juvenile growth rate, time to first reproductive activity, or fecundity (Pechenik and Cerulli 1991). In contrast, 24–48 h of osmotic stress in the larval stage of the same species affected both postsettlement survival and juvenile growth rate (Pechenik and others 2001), whereas exposure to cadmium at 1000 $\mu\text{g/l}$ affected neither postsettlement mortality nor juvenile growth rate (Pechenik and others 2001). None of these treatments affected adult fecundity in *Capitella* sp. I (Pechenik and Cerulli 1991; Pechenik and others 2001), but delaying metamorphosis did impact fecundity for the bryozoan *B. neritina* (Wendt 1998).

In addition, species seem to differ in their sensitivity. For example, delaying larval metamorphosis for as little as 1–3 h in the colonial seasquirt *D. listerianum* produced dramatic reductions in postmetamorphic colony growth (Marshall and others 2003), whereas delaying larval metamorphosis up to 48 had no apparent effect on rates of early morphological development in the solitary seasquirt *S. plicata* (Thiyagarajan and Qian 2003). The larvae of both species are lecithotrophic (yolk-feeding). Similarly, delaying metamorphosis reduced mean lophophore size for ancestrulae of the bryozoan *B. neritina* (Wendt 1996), but not for the ancestrulae of another bryozoan, *Celleporella hyalina* (Orellana and Cancino 1991), although colony growth rates were reduced for both species (Orellana and Cancino 1991; Wendt 1998).

Potential implications of latent effects in the field and laboratory

Latent effects might explain at least some of the within-species variation—and possibly much of the variation—in growth rates, survival, competitive ability, and tolerance to heat, desiccation, and pollution that have been reported in field and laboratory studies on both invertebrates and vertebrates for many decades. At least some of that variability might be due to variation in the quality of offspring arriving at particular sites, or at particular times, and that variation in quality might well be caused in large

part by experiences the animals have had as embryos or larvae.

Barnacle cyprids, for example, attach gregariously (Knight-Jones 1953), creating dense concentrations of juveniles on solid surfaces (Bertness 1989; Pechenik and others 1998). Juveniles must therefore compete for space as they grow, by crushing, overgrowing, or dislodging their neighbors (Connell 1961; Wethey 1983; Bertness 1989). Smaller juveniles may also be more vulnerable to predators and physical stresses (for example, Pechenik 1985; Miller and Carefoot 1989; Jarrett 2000; Emler and Sadro 2006). Slow growth rates should therefore put juveniles at a considerable disadvantage. Jarrett and Pechenik (1997) and Jarrett (2003) reported considerable variation in the mean growth potential of juveniles recruiting to a particular location at Nahant, MA at different times in the recruitment season over several years. The mean individual organic content of newly attached cyprids also varied among weekly cohorts of recruits in those studies. Those results are consistent with the hypothesis that larval nutritional experience or delayed metamorphosis may be affecting the quality of intertidal recruits (Jarrett and Pechenik 1997; Jarrett 2003).

Similarly, juvenile mussels (*M. galloprovincialis*—Phillips 2002) and barnacles (*Balanus glandula*—Emler and Sadro 2006) survived less well when transplanted into the field if their larvae had been food limited before metamorphosis.

The potential prominence of latent effects may call into question standard procedures for toxicity testing, as some important consequences of exposure to pollutants may not be visible until long after standard testing has ended (Heintz and others 2000; Ng and Keough 2003).

Mechanisms through which effects may be mediated

Reduced growth rates in bryozoans and colonial ascidians can be caused by a reduction in the size of food-collecting surfaces (Wendt 1996; Marshall and others 2003). For the gastropod *C. fornicata*, some data suggest that latent effects on juvenile growth are similarly caused by decreased rates of food collection (Pechenik, Jarrett, and others 2002), which in turn could be caused by abnormal gill size or function. Preliminary data suggest that reduced growth rates in juvenile barnacles may be caused by reduced dimensions of the cirral fan used in food collection (R. Emler, unpublished data; V. Thiyagarajan, P.-Y. Qian, and J. A. Pechenik, unpublished data). If so, the effects are temporary, as rates of food collection and growth increased to control levels within 1 to several weeks

after metamorphosis when juveniles were well fed (Pechenik and Jarrett 2002; Emler and Sadro 2006). But even if reduced juvenile growth rates were caused by decreased rates of food acquisition, there still remains the issue of why feeding structures were affected.

It is commonly assumed that latent effects are mediated through effects on energy stores at metamorphosis (for example, Pechenik and Eyster 1989; Pechenik and others 1993; reviewed by Pechenik and others 1998; Wendt 1998; Gebauer and others 1999; Thiyagarajan and others 2002; Marshall and others 2003). The pronounced effect of increased swimming activity on colony growth rates in colonial seaquirts (Marshall and others 2003), the difference in outcome for fed or starved larvae in the facultative planktotroph *P. sibogae* (Miller 1993), the failure to find latent effects in planktotrophic species as long as larvae are well fed during development (Pechenik and Eyster 1989; Miller and Hadfield 1990; Miller 1993), and the latent effects brought about by food limitation during larval development in some species (Pechenik, Estrella, and others 1996; Pechenik, Hammer, and others 1996; Pechenik, Li, and others 2002; Pechenik, Jarrett, and others 2002; Phillips 2002, 2004; Wacker and von Elert 2002) are consistent with this hypothesis.

However, depletion of energy stores alone may not be causing the effects observed. For example, in the solitary seaquirt *S. plicata*, although delaying metamorphosis decreased larval energy reserves by 22% over 48 h, largely through the depletion of lipid stores, no latent effects were observed in newly metamorphosed juveniles (Thiyagarajan and Qian 2003). For the marine mussel, *M. galloprovincialis*, there was no good correlation between mean larval lipid content prior to metamorphosis and juvenile performance (Phillips 2002, 2004), and for the suspension-feeding polychaete *Hydroides elegans*, fitness costs resulting from delayed metamorphosis were essentially identical whether the larvae were fed or starved during the delay period (Qian and Pechenik 1998). For the barnacle *B. amphitrite*, organic content of cyprids attaching to substrates in the field was a weak predictor of juvenile growth rate (Jarrett and Pechenik 1997).

In addition, it is difficult to explain the persistent effects of delayed metamorphosis in colonial organisms such as bryozoans and colonial ascidians based on depleted energy reserves at metamorphosis; although such depletion could account for the initial size reduction of the first zooid at metamorphosis (Wendt 1996; Marshall and others 2003) and an initially slow rate of colony development, it cannot explain the persistence of these effects as more and more zooids accumulate in the colonies (Wendt 1998; Marshall and others 2003;

Ng and Keough 2003). Why are the effects of larval experience apparently irreversible in those cases?

The mechanisms through which latent effects are mediated have been little explored. Some embryonic or larval experiences might affect transcriptional or translational processes (Pechenik and others 1998), or directly damage DNA or key enzymes (Heintz and others 2000). Among mammals, nutritional stress experienced by fetuses *in utero* can alter adult metabolism permanently, for example by altering the activities of key liver enzymes (Barker 1995; Desai and Hales 1997), apparently before the genes for those enzymes are transcribed (Barker 1995). These sorts of effects can apparently be achieved through changes in DNA methylation patterns in early development—such patterns can be influenced by embryonic nutrition (Rees and others 2000; Waterland and Jirtle 2003; Wu and others 2004).

Conclusions and open questions

Clearly, many embryonic and larval experiences, even those that are short-lived, can influence components of fitness (for example, survival, growth rates, and fecundity) in juveniles and adults in a variety of animal species from a variety of phyla. Four key questions remain to be addressed regarding these “latent effects”:

- (1) Why do some embryonic or larval experiences have latent effects on juvenile or adult performance, while other experiences, even in the same species, do not?
- (2) Why are the members of some species apparently more sensitive to those experiences than are the members of other species?
- (3) How do combinations of stresses (for example, nutritional stress and delayed metamorphosis) in early life affect the incidence and magnitude of latent effects?
- (4) To what extent do embryonic and larval experiences affect the outcomes of competitive interactions, predator-prey interactions, and exposure to physical stresses in real populations of juveniles and adults in the field? The potential impact of latent effects on population dynamics in the field is considerable, but experiments in which larvae are manipulated and reared in the laboratory or transplanted as juveniles into the field for monitoring can tell us only about that potential. For marine invertebrates in particular, we do not have any information about how often such latent effects occur in real populations, nor the extent to which they influence community dynamics in the real world.

- (5) And finally, how are latent effects mediated? What internal processes, physiological mechanisms, or molecular mechanisms cause at least some embryonic and larval experiences to have such great influence on juvenile or adult performance?

Marine invertebrates, and perhaps insects, are especially useful for such studies on latent effects, in part because the process of metamorphosis indicates a clear break between larval and juvenile life. Carefully selected invertebrate species might productively serve as general models for studying the mechanisms through which latent effects are mediated.

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