

Larval experience and latent effects—metamorphosis is not a new beginning ¹

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SYNOPSIS. For many years ecologists have documented the remarkable within-species variation inherent in natural systems—e.g., 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 UV 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 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 et al., 1998).

DEFINITIONS

The kind of effects I will be discussing in this review have recently come to be

called “carryover effects” in the ecological literature (e.g., Goater, 1994; Pakkala et al., 2001; Phillips, 2004, 2002; Marshall et al., 2003; Altwegg and Reyer, 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 (e.g., Baker, 2004; Crust, 2004; Murray et al., 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 paper 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 (e.g., Bayne et al., 1975; McCormick, 1998)—those effects already have a perfectly good name: “maternal effects” (e.g., Bayne et al., 1975; Mousseau and Dingle, 1991; Fox et al., 1995; McCormick, 1998; Agrawal et al., 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; Highsmith and Emler, 1986; Pechenik, 1985; Gaudette et al., 2001; Pechenik et al., 2002a). 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 post-metamorphic 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 [e.g., the bryozoan *Bugula stolonifera* (Woollacott et al., 1989) and the colonial seasquirt *Diplosoma listerianum* (Marshall et al., 2003)] were made to delay metamorphosis by 2-10 hours, 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 et al., 1993).

Such latent effects can persist for at least several weeks. For example, Wendt delayed the metamorphosis of *Bugula neritina* larvae for 24 h and then transplanted the colonies into the field and observed them for 2 weeks (Wendt, 1998). 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 hours resulted in significantly smaller zooid sizes for the colonial ascidian *Diplosoma 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 et al., 2003).

Other evidence for latent effects of delayed metamorphosis in marine invertebrates includes reduced juvenile survival and growth rates in a decapod crustacean (Gebauer et al., 1999), reduced postsettlement survival or reduced growth for some polychaetes and sea urchins (Highsmith and Emlet, 1986; Pechenik and Cerulli, 1991; Qian et al., 1990; Qian and Pechenik, 1998; Väitilingon et al., 2001), and reduced reproductive potential for a spionid polychaete (Qian et al., 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 et al., 1996a,b), 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,” i.e., despite our best efforts to prevent it in the laboratory (Pechenik, 1985; Pechenik et al., 2002a). 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, 1989), delaying metamorphosis of this same species for 5 days at 15 °C did not (Butman et al., 1988).

Although the larvae of at least some tropical reef fish can also delay their metamorphosis (Victor, 1986; Jenkins and May, 1994; McCormick, 1999; Cowen, 1991), there is no direct evidence for any affect 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 (Altwegg and Reyer, 2003; Relyea, 2001; Van Buskirk and Saxer, 2001; reviewed by Newman, 1992). 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 (e.g., Semlitsch et al., 1988; Altwegg and Reyer, 2003).

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

Food limitation and nutritional stress

Larvae of the nudibranch *Phestilla 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 *Crepidula fornicata* of food for 2-5 days had the unanticipated effects of stimulating metamorphosis (Pechenik et al., 1996a) and depressing rates of juvenile growth in the presence of excess food (Pechenik et al., 1996a, 1996b). 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 et al., 1998; Pechenik et al., 2002b). 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⁻¹ rather than 18×10^4 cells ml⁻¹--Pechenik et al., 1996a). In both cases, however, juvenile growth rates returned to control levels within a week after metamorphosis in several experiments (Pechenik, Jarrett, et al., 2002), suggesting that the latent effects of food limitation during larval development are temporary in this species. Similarly, initially reduced growth of juvenile barnacles (*Balanus amphitrite*) eventually returned to control levels in the presence of abundant food, but only after one to several weeks (Thiyagarajan et al., 2003; Emlet and Sadro, 2005); 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 Emlet, 1986; Miller and Emlet, 1999; Väitilingon and Morgan, 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 Emlet, 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 McEdward, 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 et al., 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 et al., 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 et al., 1976; Desai and Hales, 1997).

Salinity stress

The deposit-feeding polychaete *Capitella* sp. I showed latent effects in response to osmotic stress (Pechenik et al., 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 *Diplosoma listerianum* were forced to swim frantically for 3 hours, 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 et al., 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 et al., 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 *Crepidula fornicata* were exposed to concentrations of cadmium in seawater up to a nominal concentration of 20,000 $\mu\text{g l}^{-1}$ (Pechenik et al., 2001) for 48 h. Although many larvae died at concentrations of 2500 $\mu\text{g l}^{-1}$ or higher, some larvae survived at concentrations of up to 10,000 $\mu\text{g l}^{-1}$. 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 et al., 2001). Similar findings were reported for the polychaete *Capitella* sp. I; although the reported LD-50 for this species is about 750 $\mu\text{g l}^{-1}$ (Reish et al., 1976), exposing larvae to concentrations as high as 2000 $\mu\text{g l}^{-1}$ for up to 48 h had no effect on post-settlement survival or fecundity, and probably had no effect on juvenile growth (Pechenik et al., 2001).

Ng and Keough (2003) exposed larvae of the encrusting bryozoan *Watersipora subtorquata* to a sublethal concentration of copper (100 $\mu\text{g l}^{-1}$) 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 et al., 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 two levels of irradiation until hatching (Pahkala et al., 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 et al., 2001), whereas exposure to cadmium at 1000 µg/L affected neither postsettlement mortality nor juvenile growth rate (Pechenik et al., 2001). None of these treatments affected adult fecundity in *Capitella* sp I (Pechenik and Cerulli, 1991; Pechenik et al., 2001), but delaying metamorphosis did impact fecundity for the bryozoan *Bugula neritina* (Wendt, 1998).

In addition, species seem to differ in their sensitivity. For example, delaying larval metamorphosis for as little as 1-3 hours in the colonial seasquirt *Diplosoma listerianum* produced dramatic reductions in postmetamorphic colony growth (Marshall et al., 2003), whereas delaying larval metamorphosis up to 48 had no apparent effect on rates of early morphological development in the solitary seasquirt *Styela 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 *Bugula 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 some of the 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 et al., 1998). Juveniles must therefore compete for space as they grow, by crushing, overgrowing, or dislodging their neighbors (Bertness, 1989; Connell, 1961; Wetthey, 1983). Smaller juveniles may also be more vulnerable to predators and physical stresses (e.g., Pechenik, 1985; Miller and Carefoot, 1989; Jarrett, 2000; Emler and Sadro, 2005). 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 (*Mytilus galloprovincialis*—Philips, 2002) and barnacles (*Balanus glandula*—Emlet and Sadro, 2005) 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 et al., 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 et al., 2003). For the gastropod *Crepidula fornicata*, there are some data suggesting that latent effects on juvenile growth are similarly caused by decreased rates of food collection (Pechenik and Jarrett, 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 (Emlet, unpublished; Thiagarajan, Qian, and Pechenik, unpublished). If so, the effects are temporary, as rates of food collection and growth increased to control levels within one to several weeks after metamorphosis when juveniles were well fed (Pechenik and Jarrett, 2002; Emlet and Sadro, 2005). 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 (e.g., Marshall et al., 2003; Pechenik and Eyster, 1989; Pechenik et al., 1993; Wendt, 1998; Gebauer et al., 1999; Thiyagarajan et al., 2002; reviewed by Pechenik et al., 1998). The pronounced effect of increased swimming activity on colony growth rates in colonial seasquirts (Marshall et al., 2003), the difference in outcome for fed or starved larvae in the facultative planktotroph *Phestilla 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 et al., 1996; Pechenik et al., 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 seasquirt *Styela 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, *Mytilus 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 *Balanus 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 et al., 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 (Marshall et al., 2003; Ng and Keough, 2003; Wendt, 1998). 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 et al., 1998), or directly damage DNA or key enzymes (Heintz et al., 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 et al., 2000; Waterland and Jirtle, 2003; Wu et al., 2004).

CONCLUSIONS AND OPEN QUESTIONS

Clearly, many embryonic and larval experiences, even those that are short-lived, can influence components of fitness (e.g., 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 (e.g., nutritional stress and delayed metamorphosis) in early life affect the incidence and magnitude of latent effects?

3) 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.

4) 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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Table 1. Studies of latent effects in animals.

Taxon	Species	Treatment in larval or embryonic stage	Latent Effects?	Reference
Bryozoans				
	<i>'Hippodiplosia' insculpta</i>	Delayed metamorphosis	Yes	Nielsen, 1981
	<i>Bugula stolonifera</i>	Delayed metamorphosis	Yes	Woollacott and Pechenik, 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>Crepidula fornicata</i>	Low food concentration	Yes	Pechenik and Estrella, 1996; Pechenik and Hammer, 1996; Pechenik and Jarrett, 2002
	<i>Crepidula fornicata</i>	Cadmium	No	Pechenik and Berard, 2001
	<i>Phestilla sibogae</i>	Delayed metamorphosis	No	Miller and Hadfield,

		with fed larvae		1990
	<i>Phestilla 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 McEdward, 1990
	<i>Capitella</i> sp. I	Low salinity	Yes	Pechenik and Berard, 2001
	<i>Capitella</i> sp. I	Cadmium	No	Pechenik and Berard, 2001
	<i>Hydroides elegans</i>	Delayed metamorphosis ; Starvation	Yes	Qian and Pechenik, 1998
Crustaceans				
	<i>Chasmagnathus granulata</i>	Delayed metamorphosis	Yes	Gebauer and Paschke, 1999
	<i>Balanus amphitrite</i>	Delayed metamorphosis	Yes	Pechenik and Rittschof, 1993
	<i>Balanus amphitrite</i>	Low food concentration	Yes	Thiyagarajan et al., 2003
	<i>Balanus glandula</i>	Low food concentration	Yes	Emlet and Sadro, 2005
Insects				

	<i>Ondotoceram albicorne</i>	Increased silk usage	Yes	Stevens and Hansell, 1999
	<i>Kytorhinus sharpianus</i>	Prolonged diapause	Yes	Ishihara and Shimada, 1995
Echinoids				
	<i>Dendraster excentricus</i>	Delayed metamorphosis	Yes*	(Highsmith and Emlet, 1986
	<i>Echinarachnius parma</i>	Delayed metamorphosis	Yes*	Highsmith and Emlet, 1986
	<i>Paracentrotus lividus</i>	Delayed metamorphosis	Yes*	Vaitilingon and Morgan, 2001
	<i>Strongylocentrotus franciscanus</i> and <i>S. purpuratus</i>	Food concentration	Yes	Miller and Emlet, 1999
Urochordates				
	<i>Diplosoma listerianum</i>	Larval swimming vigor	Yes	Marshall et al, 2003
	<i>Styela plicata</i>	Delayed metamorphosis	No	Thiyagarajan and Qian, 2003
Fish				
	<i>Oncorhynchus gorbuscha</i>	Crude oil	Yes	Heintz et al., 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 et al., 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 et al., 2001
	<i>Rana lessonae</i> and <i>R. easculenta</i>	Larval density	Yes	Altwegg and Reyer, 2003
Turtles				
	<i>Chelydra serpentina</i>	Water availability	Yes	Miller et al., 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 Stein, 1976
	<i>Homo sapiens</i>	Nutritional stress <i>in utero</i>	Yes	Desai and Hales, 1997
	<i>Homo sapiens</i>	Nutritional stress <i>in utero</i>	Yes	Barker, 1995

*Results ambiguous due to high postmetamorphic mortality