Integrating function across marine life cycles

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Synopsis Complex life cycles involve a set of discrete stages that can differ dramatically in form and function. Transitions between different stages vary in nature and magnitude; likewise, the degree of autonomy among stages enabled by these transitions can vary as well. Because the selective value of traits is likely to shift over ontogeny, the degree of autonomy among stages is important for understanding how processes at one life-history stage alter the conditions for performance and selection at others. We pose 3 questions that help to define a research focus on processes that integrate function across life cycles. First, to what extent do particular transitions between life-history stages allow those stages to function as autonomous units? We identify the roles that stages play in the life history, types of transitions between stages, and 3 forces (structural, genetic/epigenetic, and experiential) that can contribute to integration among stages. Second, what are the potential implications of integration across life cycles for assumptions and predictions of life-history theory? We provide 3 examples where theory has traditionally focused on processes acting within stages in isolation from others. Third, what are the long-term consequences of carryover of experience from one life cycle stage to the next? We distinguish 3 scenarios: persistence (effects of prior experience persist through subsequent stages), amplification (effects persist and are magnified at subsequent stages), and compensation (effects are compensated for and diminish at subsequent stages). We use these scenarios to differentiate between effects of a carryover of state and carryover into subsequent processes. The symposium introduced by our discussion is meant to highlight how discrete stages can be functionally coupled, such that life cycle evolution becomes a more highly integrated response to selection than can be deduced from the study of individual stages.

Larva (lär˙ vă) *Pl.* **larvae** [L. *larva* a ghost, spectre, hobgoblin; also, a mask]

—Simpson JA, Weiner ESC, eds. *Oxford English Dictionary* Online, s.v. "larva." Oxford: Clarendon Press. 1989. *OED Online* Oxford University Press. http://oed.com.

The word "larva" first appeared in scientific writings in a life-history context when Ray (1691) appropriated the Latin term as part of an argument for halving the tally of insect species in Britain. Beetles and butterflies, he argued, should not be counted separately from the grubs and caterpillars from whence they came, since they were "the same species under a different larva, or habit." The term was applied more specifically by Linnaeus to the young stages of indirect-developing insects, for the way these stages presented a ghostly "mask" that hid the true nature of the adult form. It is now widely recognized that most multicellular organisms undergo complex life cycles (Werner 1988) with a series of stages that can differ dramatically in habitat and functional traits (defined here as aspects of the phenotype that underlie organismal performance). These differences among stages reflect some degree of functional, ecological, and evolutionary autonomy that can be reinforced by the well-defined and sometimes dramatic transitions between them.

Marine life cycles provide especially informative examples of selection operating on different functional characteristics associated with different life-history stages. For example, marine taxa commonly face challenges to fertilization of free-spawned gametes, to nutrient acquisition during pelagic larval development, to benthic site selection and juvenile survival, and to adult reproductive location and timing. The recognition of ontogenetic shifts in functional roles is fundamental to understanding ecological and evolutionary processes at the organismal and population levels, because the nature and strength of selective pressures can change more dramatically within life cycles than among adults of different species (Werner and Gilliam 1984).

Metamorphosis has traditionally been viewed as a means of decoupling the phenotypic traits required to

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meet functional challenges during different parts of a life cycle (Wilbur 1980). Recent evidence, particularly from the marine literature, however, indicates that consequences of variation in performance at one life-history stage can "carry over" into significant effects on later stages. For example, characteristics of eggs that influence fertilization success can determine the distribution of larval traits (Marshall and others 2002; Marshall and Keough 2003b); embryonic experience can alter larval and juvenile performance (Moran and Emlet 2001; Giménez and Anger 2003); planktonic larval experience can influence benthic juvenile success (Qian and Pechenik 1998; Pechenik and Rice 2001; Phillips 2002; Giménez and others 2004); and adult reproductive timing or location can alter developmental conditions for offspring (Brawley and others 1999; Podolsky 2003). These examples suggest that life cycle evolution is a more highly integrated response to selection than can be deduced from the study of individual stages. Nevertheless, traditional models of life-history evolution (for example, Vance 1973; Smith and Fretwell 1974; Christiansen and Fenchel 1979) and their derivatives have tended to examine stages in isolation.

In the symposium that we introduce with this paper, we aimed to draw together and synthesize recent and ongoing research on organismal performance at different life-history stages—gametes, embryos, larvae, juveniles, and adults—that emphasizes relationships among these stages. In particular, we aimed to highlight research that has been innovative in demonstrating how events or processes at one life-history stage can alter the conditions for performance and selection at others. Here, we briefly outline some broad themes that motivated our invitations to speakers who work on disparate organisms, life-history transitions, and research questions. Our goal is to provide not a comprehensive review of the topic (see other contributions to this symposium and Pechenik [2006]) but rather to present some opening perspectives on 3 questions that we feel help to define a research focus on processes that act to integrate function across life cycles.

What degree of autonomy is enabled by different life-history transitions?

Stages of a highly generalized, complex marine life cycle (Table 1) can be viewed as playing different functional roles: gametes rely on chemistry and physics to make contact and achieve fertilization; embryos undergo rapid cell division and morphogenesis and set up patterns of cell differentiation and body organization; larvae transform acquired nutrients into growth, disperse, and locate appropriate sites for settlement; juveniles complete metamorphosis, recruit to nursery, or adult habitats, and undergo the majority of growth to reproductive maturity; and adults shift allocation from growth toward gametogenesis and reproduction. Many variations on this generalized life cycle exist, but they are all constrained by the need to transform a small, relatively featureless zygote into a large, complex, reproducing adult, only to be constrained again to pass through a single-cell stage (Grosberg and Strathmann 1998). Because the selective value of traits that support many of these roles is likely to shift over ontogeny, the discrete stages of a life cycle can be expected to evolve, with the assumption of some degree of autonomy, in response to different selective forces. In this sense, a traditional view of life-history stages casts them as "modules" (*sensu* Schlosser and Wagner 2004), with a high degree of integration within stages and of autonomy between stages.

While our generalized summary of functional roles among stages is broadly applicable, defining the degree of autonomy enabled by transitions between stages is less straightforward. How much does a given transformation allow a stage to escape constraints on form or function that acted at previous stages, or that will appear at later stages? In Table 1 we depict some traditional views of the degree of autonomy between stages based on the transformation of *structure*. For example, the transition between larva and

Table 1 Stages of a generalized complex marine life cycle representative of a typical invertebrate species with planktotrophic development

Life-history stage	Functional role	Transition	Degree of autonomy enabled by transition
Gamete	Contact, fertilization	Cell division	+++
Embryo	Rapid cell division, morphogenesis	Hatching	++
Larva	Feeding, growth, dispersal, settlement	Metamorphosis	+++
Juvenile	Recruitment, growth	Maturation	+
Adult	Growth, reproduction	Gametogenesis	++++

Many variations are possible not only within invertebrates but also across fishes and algae, taxa that were also considered in this symposium. The final column is meant to depict traditional views of the degree of autonomy conferred by each life-history transition, based on the description of structural integration in the text.

juvenile can allow a high degree of autonomy because metamorphosis often provides a radical reorganization of body design. In contrast, the transition from juvenile to adult often involves a more gradual process of sexual maturation, with many adult structures (other than gonads) already in place in the juvenile. (Colonial ascidians provide an important counterexample to this traditional view. Many adult structures have already partly or fully differentiated by the time of metamorphosis, unlike in solitary ascidians; thus, the degree of structural autonomy between stages can be affected by shifts in larval developmental mode [see Davidson and others 2004]). We have also assigned high autonomy scores to gametogenesis (adults do not resemble their eggs) and early cell division (eggs from different taxa look similar but give rise to different early patterns of cell division and morphogenesis) and an intermediate score to hatching (Table 1). We expect these choices—based strictly on the degree of structural reorganization at each transition—not to be without controversy, and offer them only as a starting point for discussion of forces that can integrate function across discrete stages.

In addition to this traditional focus on structural integration—which involves the retention, loss, or alteration of structures during transitions—life cycles can be functionally integrated by at least 2 other forces. First, the same genes may be active at 2 or more stages, a force we refer to as genetic/epigenetic integration (recognizing that epigenetic processes that alter gene expression without altering base sequences can also act to integrate phenotypic expression across stages). We distinguish structural from genetic/epigenetic forces because structural continuity can occur with or without the same genes being active at 2 life-history stages, while genes may be active at 2 stages without influencing the same structures. Second, and most importantly for our discussion, we emphasize the role of experiential integration—the potential for "carryover" of effects of experience during one life-history stage into performance and selection at subsequent stages. The research described below and featured in this symposium is intended to focus primarily on carryover of experiential effects. With this focus, we offer a perspective on integration among stages that is different from the traditional focus on changes in structural design.

These 3 sources of life cycle integration may also interact in important ways. For example, Giménez's (2006) contribution to this symposium describes a case where experience at one stage can alter patterns of gene expression at a subsequent stage, modifying the degree to which 2 stages have developmental processes with a common genetic basis.

How can recognition of "carryover effects" influence traditional assumptions and predictions of life-history theory?

Life-history theory comprises a set of models that address major lifetime transitions in the use or allocation of resources, including nutrients, energy, time, and space. Because complex life cycles involve discrete stages, one general and convenient assumption in many such models is that stages can be treated in isolation. For example, the highly influential "time-fecundity" model of the evolution of reproductive mode, developed by Vance (1973) and refined by others (for example, McEdward and Miner 2003; Kiflawi 2006), was based on the assumption that survival benefits, which are traded off against the fecundity costs of producing larger eggs, are restricted to processes during the larval stage. Recent work has emphasized the additional consequences of egg-size variation for fertilization processes preceding the larval stage (Levitan 1993, 2000; Podolsky and Strathmann 1996; Styan 1998; Podolsky 2004) and of variation in egg size and larval experience for postsettlement processes following the larval stage (Emlet and Hoegh-Guldberg 1997; Allen and others 2006). More generally, if the effects of prior experience convey across life-history transitions, what are the implications of this source of integration for life-history theory? To consider this question, we examine 3 common assumptions of theory and how they may be altered by the recognition of carryover effects.

First, investment per egg is commonly assumed to evolve toward an optimum in response to rates of larval mortality in the plankton, which are regulated by factors such as temperature, predation, and food availability (for example, Vance 1973; Smith and Fretwell 1974; Levitan 2000; Marshall and Keough's [2006] contribution to this symposium). A corollary of this assumption is that within species, changes in adult resource availability should have a greater effect on egg number than on egg size. The first part of this scenario, that egg size evolves in response to larval conditions, is well supported (for example, Cushing 1967; Bagenal 1971; Thresher 1982). For example, the closure of the Isthmus of Panama resulted in the separation of many pairs of closely related "geminate" species (Jordan 1908) in which 1 species inhabits the high-productivity eastern Pacific Ocean and its geminate inhabits the low-productivity western Atlantic ocean. In several of these geminate pairs, the Pacific species has smaller eggs than does the Atlantic one (for example, echinoid and asteroid echinoderms [Lessios 1990], and arcid bivalves [Moran 2004]), supporting

the idea that a higher-quality larval feeding environment selects for smaller eggs. This pattern of variation in egg size holds between oceans, although not in comparisons between animals or populations exposed to variation in local or seasonal productivity (A. Moran, unpublished data).

In contrast, other studies suggest that within species, variation in egg size may not be related to the conditions larvae are likely to experience. In some taxa, egg size can be influenced by size or age of the female (Marshall and others 2000; Bingham and others 2004; Hemmi and Jormalainen 2004; Marshall and Keough 2004a), by temperature or salinity experienced during oogenesis (Giménez and Anger 2001; Fischer and others 2004), by the availability and quality of food in the female diet (Bayne and others 1978; George 1996; Hemmi and Jormalainen 2004), or even by paternal characteristics (Galeotti and others 2006). Regardless of why egg sizes differ, offspring produced from smaller eggs generally show lower survival and reduced performance, either across populations or within broods from individual mothers (Giménez and Anger 2001; Marshall and Keough 2003a; Marshall and others 2003; but see Moran and Emlet 2001). Thus, many aspects of the maternal environment can carryover into effects on survival and performance at the larval stage through their effects on egg size. Furthermore, such effects can be pervasive and long-lasting; the negative impacts of small egg size can propagate through the larval stage to the juvenile and adult stages (Marshall and others 2003; Giménez and others 2004; Marshall and Keough 2004; Marshall and others 2006) and may lead to population-level effects, as described by Giménez (2006) in his contribution to this symposium. Traditional optimality models do not address either the presence of nonadaptive intraspecific variation in egg size, or the propagation of egg-size effects throughout the life cycle. Incorporating carryover effects into such models may lead to a better understanding of how these effects may influence population dynamics and the evolution of life histories.

A second implicit assumption of traditional life-history theory, including the time-fecundity model, concerns the related ideas that fertilization rates are independent of investment per offspring, and that offspring size is not affected by fertilization conditions. As first demonstrated by Rothschild and Swann (1951) and later revived in a life-history context by Levitan (1993), fertilization success of a given egg can in fact depend on the size of the target it presents to sperm (see also Podolsky 2001, 2002; Farley and Levitan 2001). Marshall and colleagues (2002) demonstrated that the "sperm environment" experienced by eggs can further alter larval characteristics, because larger larvae resulted from larger eggs that were preferentially fertilized in sperm-limiting environments, and smaller larvae resulted from smaller eggs favored in sperm-saturated environments (presumably through avoidance of polyspermy risk). In this case, realized larval size was determined not by selection for some size-related factor at the larval stage related to predation, feeding, or starvation, but rather by the egg size that was optimal at under fertilization conditions at the time of spawning. The interaction between egg size and fertilization success provides another example of the complex links between life-history stages that can alter the assumptions of basic life-history models.

Third, a number of models have assumed, either implicitly or explicitly, that size at metamorphosis is independent of egg size, at least for planktotrophic species (for example, Vance 1973; Levitan 2000). By decoupling premetamorphic and postmetamorphic processes, this assumption allows theoretical models to address the larval stage in isolation without regard for potential postmetamorphic effects of egg size or larval experience. One important outcome of incorporating this assumption into life-history models is that, all else being equal, larvae from smaller eggs should require more time in the plankton to gain the resources needed to reach a suitable "critical" size for metamorphosis. For some taxa, egg size and size at metamorphosis do indeed appear to be independent (Emlet and others 1987; Levitan 2000; R. Podolsky and J. Allen, unpublished data). Within species, however, some studies suggest that larval food availability can directly influence settlement size (Allen and others 2006) and can even drive an inverse evolutionary relationship between egg size and settlement size (A. Moran, unpublished data). This inverse relationship may result from the evolution of growth rates in response to contrasting environments. For example, arcid bivalves that develop in the high-productivity eastern Pacific have smaller eggs than do their geminates in the western Atlantic, but grow to larger sizes at metamorphosis (Fig. 1). Similarly, Giménez and colleagues (2004) demonstrated that crustacean larvae from smaller eggs were routed into a longer developmental pathway (and a longer planktonic feeding period) than were those from larger eggs, resulting in larger sizes at metamorphosis. Thus, selection during the larval feeding stage can result in an evolutionarily driven or physiologically driven inverse relationship between egg size and size at metamorphosis that was not adequately considered in traditional models of marine life-history evolution.

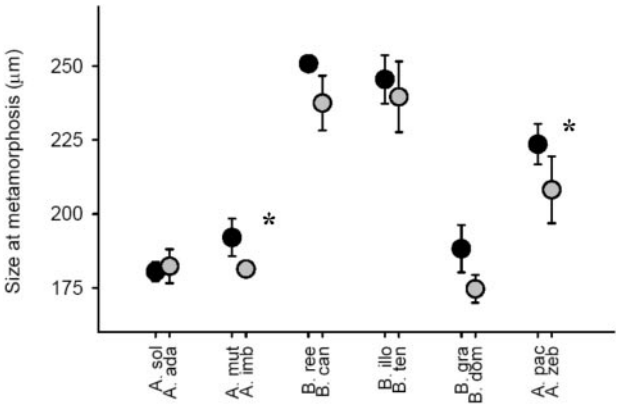

Fig. 1 Size at metamorphosis (= length of prodissoconch II) of 12 species of arcid bivalves from 6 geminate pairs. In each pair, 1 species inhabits the high-productivity eastern Pacific (black circles) while its geminate inhabits the low-productivity western Atlantic (gray circles). Settlement sizes are larger in the Pacific species in 5 out of 6 pairs. Sample sizes range from 1 (*B. ree*) to 6 individuals per species; error bars are standard deviations. Asterisks indicate pairs which differ significantly from each other at the $P = 0.05$ level (Student's *t*-test). Full names of species, characteristic egg sizes, collection localities, and scanning electron microscopical techniques are described by Moran (2004).

Does carryover of effects from prior experience have long-term consequences?

The examples described above demonstrate that experience at one life-history stage can influence traits or processes at subsequent stages, with the potential for long-term effects on organismal performance and fitness. The mere appearance of such effects at the start of a subsequent stage, however, does not necessarily indicate what their significance will be for subsequent performance. We consider 3 scenarios in which carryover effects simply persist over time (= *persistence*), are augmented during subsequent stages (= *amplification*), or are alleviated (or even reversed) by compensatory effects (= *compensation*). Because one goal of studying carryover effects is to integrate the consequences of experience over a life cycle, it is useful to formally distinguish among these scenarios.

The 3 outcomes described above are formalized using an example, illustrated in Figure 2. Because size and growth are central parameters in many life-history models, we use body size or condition as the manifestation of an effect carried over from the embryonic to larval stage; other effects and stage transitions, of course, are possible. Size is presented on a log scale so that equal slopes represent equal proportional rates of growth. In this example, 2 groups experience different conditions during embryonic development (stage s_E, bounded by fertilization [t_F] and hatching [t_H] as transitions) that lead to differences in size at the start of the larval stage, s_L. Thereafter, the 2 groups are represented as experiencing common conditions in order to isolate the effects of experience during s_E. Under a scenario of persistence (A), the difference in size persists but neither increases nor decreases appreciably during s_L. This scenario can be viewed as reflecting a carryover of state—that is, experience during s_E has an initial and lasting effect on size through stage s_L, but does not appear to further influence processes that determine size by the end of s_L. In contrast, under a scenario of amplification (B), experience during s_E appears to carryover not only into the initial state but also into processes that affect growth during s_L. In this sense, the effects of prior experience persist and appear to be magnified, even in the absence of differences in treatment during s_L. Finally, in a scenario of compensation (C), initial differences in state diminish over the course of s_L, as a result of compensating processes that influence growth during that stage of the life cycle. Similar analyses of carryover effects could be carried out for all transitions in the life cycle, generating matrices of values that define the effects of life-history experiences at one stage on states and processes at subsequent stages. Below, we give examples of real data consistent with the 3 scenarios described above.

Persistence

One example of persistence comes from work by Podolsky and colleagues on the intertidal opisthobranch mollusc *Melanochlamys diomedea*. Adults of this species inhabit soft-bottom tidal flats where they oviposit gelatinous egg masses during the late spring and summer. While adults can regulate their own body temperatures by burrowing under the surface, embryos contained in the gelatinous masses are tethered on the surface within tidal pools, where they experience fluctuations in temperature. Temperatures in tide pools surveyed with small data loggers show that maximum temperatures experienced by embryos regularly exceed the threshold for heat-shock protein expression (~26°C). In the laboratory Podolsky (2003) exposed the encapsulated embryos to sets of different daily fluctuating temperature profiles that mimicked the rise and fall of field temperatures, with temperature peaks ranging among treatments from 20 to 34°C. These treatments generated a bell-shaped thermal-performance curve for hatching size, with maximum hatching sizes at an intermediate, nonstressful peak temperature (24°C) and smaller sizes at higher or lower temperatures. Hatchlings treated in this way were then reared

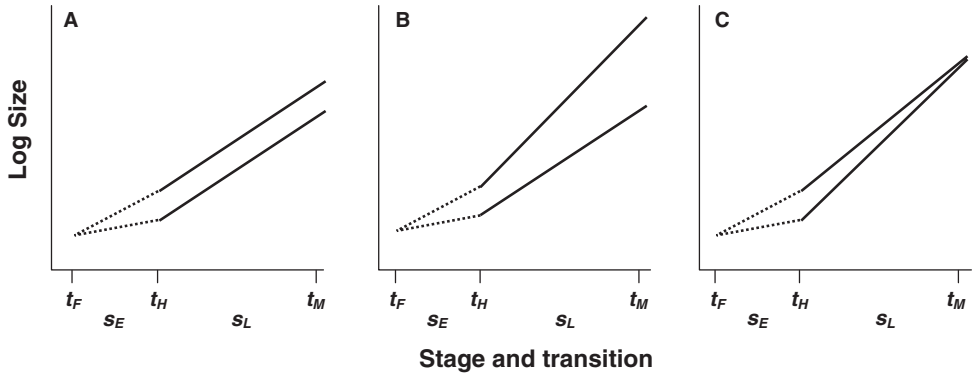

Fig. 2 Three scenarios depicting different hypothetical long-term consequences of carryover effects on organism size. In this example, 2 life-history stages, s_E and s_T (periods of embryonic and larval development, respectively), are bounded by transitions t_F, t_H, and t_M (fertilization, hatching, and metamorphosis, respectively). In each case, treatments differ between the 2 plotted lines during life-history stage s_E but are the same during s_L, in order to identify the effects of experience during s_E on growth and size during s_L. (**A**) Persistence: differences in treatment during s_E lead to differences in size that persist through s_L. (**B**) Amplification: differences in treatment during s_E continue to influence relative growth rate during s_L, thereby amplifying the effects prior experience. (**C**) Compensation: processes underlying growth during s_L compensate for effects of differences in treatment during s_E. Size is plotted on a log scale to show proportional changes in growth.

by R. Podolsky and M. Mach (unpublished data) through larval development in a common environment, to determine whether the effects of embryonic experience persisted during planktotrophic larval development and further influenced larval growth. We found that hatchlings from all treatments experienced approximately the same size increase (~80%) during 2 weeks of larval development (Fig. 3), suggesting that carryover of size effects persisted but were not magnified by processes during the larval stage. This result is a first step toward understanding whether the effects of heat stress experienced by intertidal embryos have consequences for lifetime survival or reproduction.

As another example of persistence, Moran (1999) investigated the postmetamorphic consequences of hatching size in *Nucella ostrina*, a direct-developing intertidal gastropod whose embryos feed on nurse eggs in the capsule and show substantial within-clutch variation in offspring size. In this study, the effects of hatching size persisted for several months in the juvenile stage, but all hatchlings, regardless of initial size, appeared to be on the same growth trajectory (Fig. 4). Thus, the long-term effects of hatching size on growth (and hence size-at-age) persisted for long periods but were not amplified; small hatchlings did not compensate for their small initial size by growing more rapidly than their larger siblings. Likewise, all juveniles at a given size grew at similar rates regardless of their initial hatching size, suggesting no long-term negative impacts of small initial size on intrinsic growth rate.

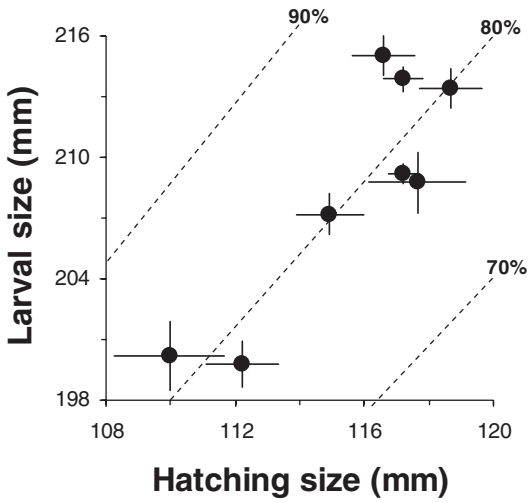

Fig. 3 Change in size (maximum shell length) after 2 weeks of planktotrophic larval development following hatching in the mollusc *Melanochlamys diomedea*. Each point represents the mean hatching size ± SE for 6 cultures for a given treatment applied during the embryonic phase [see text for description of treatments of embryos; experimental details are similar to those given by Podolsky (2003)], as well as sizes of larvae from those cultures after 2 weeks of rearing under common conditions (R. Podolsky and M. Mach, unpublished data). Larvae were fed saturating concentrations of unicellular algae.

Amplification

A study by Marshall and colleagues (2003) on the ascidian species *Diplosoma listerianum* demonstrated how the effects of prior experience can persist and be

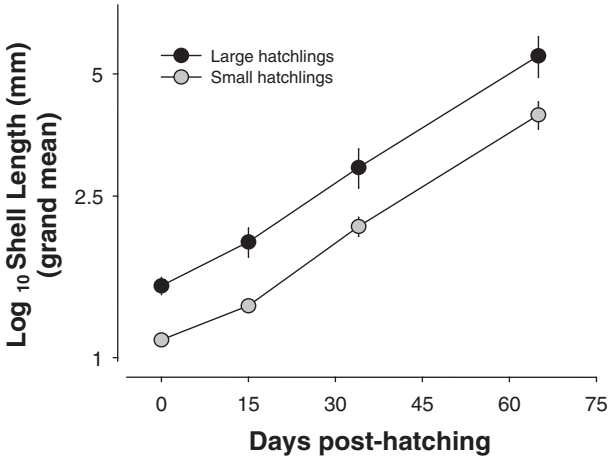

Fig. 4 Persistence of differences in hatching size of the intertidal gastropod *Nucella ostrina*. Symbols represent the grand means of large (black circles) and small (gray circles) sibling hatchlings from 6 separate clutches reared in a common laboratory environment for >2 months and fed *ad libitum*. Complete methods are described by Moran (1999). Adapted from Moran's (1999) Figure 2.

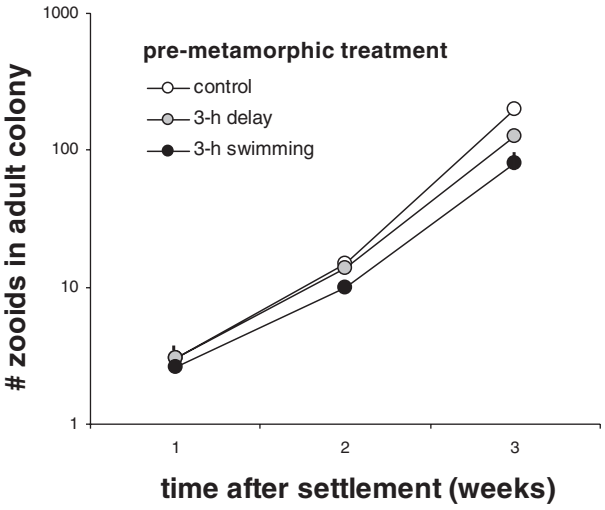

Fig. 5 Changes in mean colony size of the colonial ascidian *Diplosoma listerianum* following settlement. Treatments involved natural metamorphosis (control, $N = 14$ colonies), an induced 3 h delay of metamorphosis (3 h delay, $N = 17$), and an induced 3 h delay of metamorphosis during which swimming was continually induced by response to sudden changes in light [swimming for 3 h ($N = 9$)]. Redrawn from Figure 4 in Marshall and colleagues (2003), with data plotted on a $\log_{10}$ scale. Error bars (±1 SE) are mostly smaller than points.

magnified by processes at later life stages. In that study, larvae were either allowed to metamorphose soon after release from the adult, were forced to expend additional energy by delaying metamorphosis for an additional 3 h, or were delayed by 3 h and forced to expend even more energy by swimming. Lengthening the larval period and increasing larval energy expenditure each dramatically reduced the growth rates of metamorphosed juveniles and continued to have substantial downstream effects on the colonies produced by these larvae, which added zooids at a slower rate (Fig. 5) and with smaller feeding structures. Thus, individuals that expended more energy as larvae paid mounting long-term costs as shown by reduced performance of juveniles and adults.

Compensation

A handful of experiments have demonstrated compensation, that is, a "catching up" in size by smaller offspring under the influence of external processes that influence growth or place constraints on the adult stage. As one example, Marshall and Keough (2004b) investigated the link between larval size and postmetamorphic growth in the bryozoan *Watersipora subtorquata*. While metamorphs from larger larvae initially grew faster than did metamorphs from small larvae, after several weeks in the field there was no relationship between larval size and colony size. This effect was attributed to competition for space from other organisms, which limited the size to which adult colonies could expand. In this example, despite differences in postmetamorphic growth rate between juveniles from large and small larvae, there was no carryover of size from larval to adult stages because the link between larval size and adult size was severed by interspecific competition for space. The benefits of large larval size may have been redirected, however, toward the enhancement of other adult characteristics.

Another type of compensation pertains to the feeding conditions that regulate growth rates of larvae of planktotrophic species. Larval feeding environment can have evolutionary effects on egg size, such that planktotrophic species produce smaller eggs in regions of long-term higher productivity (Thresher 1982; Lessios 1990; Moran 2004). In the study of tropical American arcid bivalves described above, Moran (2004) and A. Moran (unpublished data) found that egg size and settlement size were inversely related; species in high-productivity regions generally had both smaller eggs and larger sizes at metamorphosis than did species from regions of low productivity (Fig. 1). In this example, environmental effects likely compensated for low maternal investment-per-offspring through greater availability of food for larvae. Another example of compensation comes from the study by Giménez and colleagues (2004) described above, in which an inverse relationship between egg

size and length of the larval feeding period caused larvae from smaller eggs to metamorphose into larger juveniles. In this example, larvae that began at small size could compensate and erase their initial size deficit by increasing the duration of larval development, thus increasing the period of time available for feeding and growth prior to metamorphosis.

The sometimes dramatic transitions between stages of the life cycle—involving fertilization, hatching, metamorphosis, maturation, and gametogenesis—can provide a substantial degree of evolutionary and ecological autonomy among stages. Yet, as the examples given above and the work of other participants who contributed to this symposium demonstrate, carryover is also a fundamental underlying force acting to shape the complex life cycles of marine organisms. Carryover effects have been demonstrated in multiple phyla; they occur between contiguous stages in many parts of the life cycle and even connect across multiple stages; and they have at least occasional strong effects on the dynamics of higher levels of biological organization, such as populations and communities. One emerging theme is that the strength of these effects is also mediated by environmental or biological contexts. As we see them, 2 exciting challenges to life-history biologists working in the marine realm are now (1) to fit these ideas into the explanatory theoretical frameworks that have shaped so much of life-history theory, but have often considered each life-history stage to be largely independent of others, and (2) to understand the influence of carryover effects on performance and selection both over the entire life cycle, and over broad ecological and evolutionary timescales.

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