

Legacies in life histories

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Synopsis Complex life-histories are common in nature, have many important biological consequences, and are an important focal area for integrative biology. For organisms with complex life-histories, a legacy is something handed down from an ancestor or previous stage, and can be genetic, nutritional/provisional, experiential, as well as the result of random chance and natural variation in the environment. As we learn more about complex life-histories, it becomes clear that legacies are inexorably linked in the short- and long-term through ecology and evolution. Understanding the consequences and drivers of life-history patterns can therefore only be understood by considering all types of legacies and integrating legacies across the entire life cycle. Larry McEdward was a leader in the field of ecological physiology, and evolutionary ecology of marine invertebrate larvae with complex life-histories. Through his scientific work and publications, devotion to students, colleagues, family, and friends, Larry has left a lasting legacy that will impact the future development of the field of larval ecology and complex life-histories.

Introduction

Complex life-histories are an important focal area of study that integrates across disciplines including ecology, evolution, development, physiology, and behavior. They are common in nature, found in almost all major taxa of both plants and animals, and have many important biological consequences. Among animals, the greatest diversity of life histories is found in marine invertebrates. Virtually all animal phyla originated in marine systems and have a larval form (Levin and Bridges 1995; Young and others 2002). Evidence suggests that the ancestral condition for many animal phyla is a complex life-history (Jägersten 1972; Nielsen 1995). These complex life-histories result in early life stages that are physiologically, morphologically, and ecologically different from later stages. Furthermore, there are intriguing phylogenetic patterns of complex life-histories among species of marine invertebrates—including convergence of adult forms with different larval types, and convergence of larval forms with different adults. It is therefore not surprising that complex life-histories of marine invertebrates have fascinated scientists since the mid-1800s when Thompson discovered the larvae of crabs and barnacles (see Young 1990 for an excellent review of the history of larval ecology), and have proven to be vital for

studies of physiology, life-history theory, ecology, and most recently evolution of development and biogeography.

Larry McEdward was a leader in the field of ecological physiology, and evolutionary ecology of marine invertebrate larvae, until 2001 when he unexpectedly passed away—a significant loss to the field. As a tribute to Dr. McEdward, we assembled leaders in the studies of complex life-histories of marine invertebrates for a symposium held at the annual meeting of the Society for Integrative and Comparative Biology in San Diego, California in January of 2005. This symposium combined forward thinking syntheses of ideas for guiding future studies of complex life-histories of marine animals. Since the last major review of this area (McEdward 1995) there have been several major advances in our understanding of complex life-histories in marine invertebrates, including the ecological forces that drive evolutionary shifts in life histories, the developmental mechanisms that allow for these shifts, the ecological and evolutionary roles of dispersal via larvae, and the linking of larval condition with later life-history stages. The papers derived from our symposium and contained in this volume synthesize recent major research advances, and focus on the future directions, especially those that result from Dr. McEdward's work. We hope

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that this collection facilitates new questions and lays the foundation for work on complex life-histories for the next several decades.

Legacies in marine invertebrate complex life-histories

A general concept that emerged from the symposium was the importance of different types of legacies for the evolution and ecology of complex life-histories. According to The American Heritage Dictionary (2000) a legacy is something handed down from an ancestor, a predecessor or from the past. The origin of legacy comes from the Medieval Latin *legatio* and from Latin *legare*, which mean to bequeath. For larvae resulting from complex life-histories there are many types of legacies (Fig. 1), 3 of which seem particularly important: genetic, provisioning, and experiential legacies.

Genetic legacies

The genetic composition of an individual is a legacy bequeathed directly from parents, and ultimately through phylogenetic contributions of ancient ancestors (Fig. 1). Understanding the causes for and consequences of genetic legacies has been a primary goal of studies of life history, such as the evolution of life-history traits within lineages (Byrne 2006; Zeng

and others 2006) and the patterns of development and mechanisms that alter gene expression and function (Wray 2006). In addition, genetic legacies can be used as a tool to reconstruct long-term evolutionary histories, which can then be used to examine broad scale patterns of dispersal and range expansion (Paulay and Meyer 2006). For example, Byrne (2006) has been able to reveal a stunning diversity of life histories among closely related Asteroids in southern Australia. She has also shown that this life-history diversity is seen in very closely related species with similar morphologies, some so similar that they form cryptic species pairs. This work clearly shows that life-history stages can be extremely labile and decoupled through evolutionary time, and thus do not necessarily change in a unidirectional pattern as had previously been assumed. Life history and growth form also show repeated evolutionary origins in ascidians (Zeng and others 2006), and it is genetic and phylogenetic legacies that allow us to unravel these historic patterns.

Thus, although there is some element of phylogenetic inertia in many aspects of the development, morphology, and behavior driven by historic genetic legacies, variation in genetic mechanisms that impact development and function in the present shows

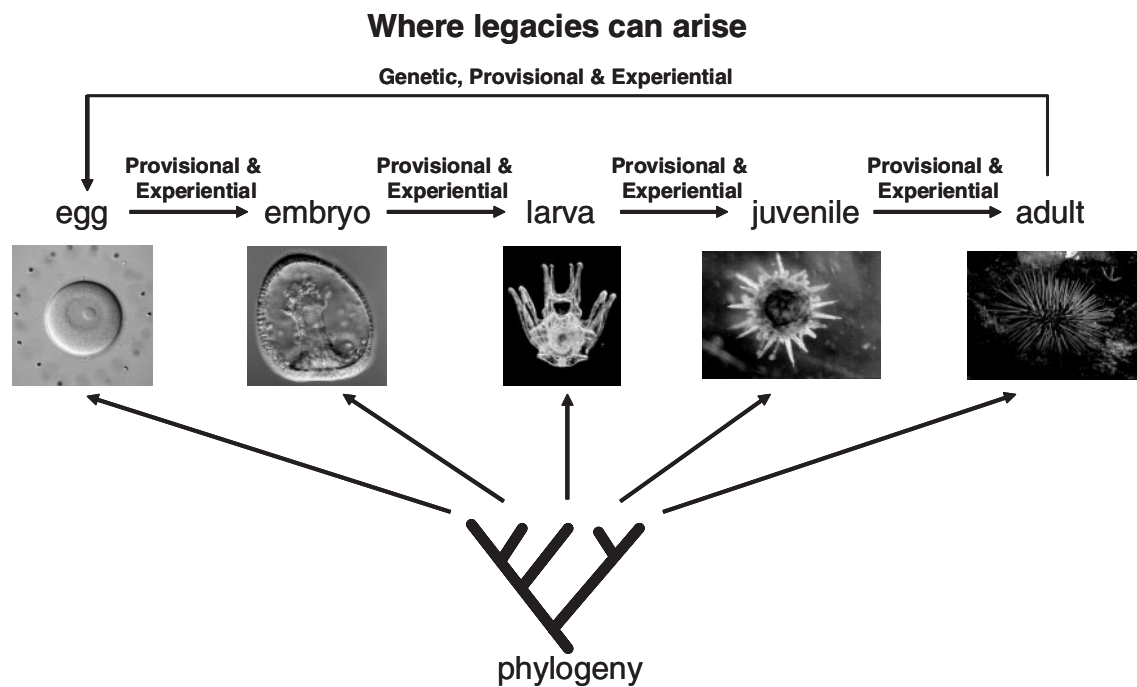


Fig. 1 Legacies can arise at a variety of different stages within a life history. For the complex life-cycle of sea urchins, arrows indicate where genetic, provisional, and experiential legacies can arise. After a legacy arises it has the potential to influence any subsequent stage, including stages of future generations. Legacies are not just short term. Any type of legacy that impacts survivorship and fitness in past generations can influence current and future generations, especially through genetic legacies.

that these features can be labile, allowing similar mechanisms to operate in different ways, as well as converge of form with a divergence of function (Wray 2006). Certainly much of the work on the evolution of development (EvoDevo) has shown that genetic legacies provide the opportunity for flexibility as well as constraints that can drive alternative strategies and solutions.

Provisioning legacies

Provisions (materials including energy, nutrients, etc.) acquired during a life stage and passed on or provided to (for example, nurse eggs) a subsequent stage are also an important legacy in complex life-histories (Fig. 1). An obvious provisional legacy is the parental material and energy contributed to eggs, which can affect subsequent development, such as whether an egg is fertilized (Levitan 2006), or when larvae must feed to avoid starving (McEdward and Miner 2006). Because much of the theory developed to explain the evolution of different developmental modes in marine animals has focused on the importance of egg size (Vance 1973), and therefore maternal provisioning, the effects of provisional legacies demand further attention (see McEdward 1997; Levitan 2000).

Energy and nutritional provisioning to eggs impacts egg size, which can impact fertilization success (Levitan 2006), as well as development time and the need for larval feeding (McEdward and Miner 2006), which impact dispersal potential (Paulay and Meyer 2006; Levin 2006) and has been the focus of life-history models (Havenhand 1995; McEdward and Miner 2006). There has also been recent recognition that some larvae have facultative feeding, and that lecithotrophic and planktotrophic life histories are not distinct categories. Therefore, larval feeding mode is not necessarily dictated by genetics, but can be flexible and dependent on environmental conditions as well as the nutritional legacies of parental investment. These new findings dictate the need for a revision and re-evaluation of how we approach life-history models (McEdward and Miner 2006).

Although provisional legacies almost certainly have important consequences throughout ontogeny for organisms with complex life-histories, relatively few of these legacies have been investigated. One type of provisional legacy that is starting to receive more attention is how nutritional stores accumulated as larvae influence post-metamorphic juvenile size, growth and performance (Emler 2006; Pechenik 2006). This work clearly demonstrates that we need to include ontogeny after the larval stage when considering complex life-histories. Having enough energy or nutritional stores just sufficient for metamorphosis is not the end of the

story—the amount, and perhaps quality, of resources that larvae acquire can influence the success of later life stages (Emler 2006; Pechenik 2006). Equally important are the potential tradeoffs that larvae face between gathering nutrition and other demands such as locomotion (Strathmann and Grünbaum 2006), which will impact the amount of provisional legacy that a larva can accumulate for later life stages. The importance of provisional legacies for later life stages is potentially not only important for species with feeding larvae, but also for those with non-feeding larvae, especially depending on the length of the larval phase, and environmental conditions. However, this question has yet to be explored for those species with non-feeding larvae.

Environmental/experiential legacies

Environmental or experiential legacies result from experiences during ontogeny that influence later stages (Fig. 1). For example, the large distance dispersal of many larvae is determined by water currents that carry them into waters with different types of characteristics, thus the larval experience can be quite variable among individuals within the same species, and sometimes among individuals within the same population (Levin 2006). Many larvae have been shown to be capable of phenotypically plastic responses to short-term variability in the environment, and these responses can have not only short term but also lasting impacts (Hadfield and Strathmann 1996). Miner and Vonesh (2004) demonstrated that larvae can not only alter their morphology in response to the mean difference in food concentration, but also to the amount of variation in food concentration. Larvae reared on a constant diet developed larger feeding structures than those fed the same mean density of food, but that experienced higher variance in food concentrations, as might be expected in the real world given the patchiness of natural phytoplankton populations. Exposure to predators during the larval phase can also impact behavior and morphology, including shell growth and thickness in gastropod larvae (D. Vaughn, unpublished data). Such short-term changes due to phenotypically plastic responses will have a lasting legacy on individuals, especially as they may impact factors important for feeding efficiency, locomotion, growth, and survivorship during the larval phase.

Experiences and local environmental fluctuations and conditions can affect all life stages and can impact such important life-history features such as phenology, age, and size of first reproduction, number of reproductive bouts, as well as persistence and longevity (Hadfield and Strathmann 1996). Environmental and experiential legacies have received the least amount of

attention to date, but are undoubtedly important for the evolution of complex life-histories.

Integration among types of legacies

Each type of legacy does not operate in isolation, but rather in concert with all other legacies throughout the life history of an individual (Fig. 1). Each provides and responds to feedbacks, opportunities, and constraints of the others. Legacies link all different life-history stages, therefore focusing solely on eggs or larvae is not sufficient. In addition, different types of legacies interact and therefore an integrative approach that considers how the combined effects of different legacies influence the evolution and ecology of species with complex life-histories is needed.

Parental experience and physiological state can alter the allocation of provisional legacies to offspring, thus changing important life-history parameters such as development time and whether or not larvae need to or can feed in the plankton (Gibson and Gibson 2004). The length of the larval phase can have a number of impacts, including the potential for dispersal, range expansion, and larval transport (Levin 2006; Paulay and Meyer 2006). Feedbacks between provisional and experiential legacies can impact large scale patterns of dispersal and biogeographic patterns, both of which are currently important for conservation, patterns of biodiversity, as well as local enhancement and recovery of species in protected areas and for fisheries enhancement and restoration (Levin 2006).

Morphological legacies also have impacts on larval performance and post-larval life-history. At a basic level, morphology is genetically controlled, and the result of long evolutionary histories of body plans and larval forms (Raff 1996). Environmentally induced feedbacks can modulate larval morphologies (through phenotypic plasticity, for example, Miner and Vonesh 2004) and behaviors that then further impact performance and energy or nutritional acquisition as well as survivorship. Indeed, the contrasting tradeoffs between alternative necessities of planktonic larvae such as locomotion and feeding (Strathmann and Grünbaum 2006) can impact developmental morphology and larval nutritional acquisition, both known to drive and be driven by feedbacks between the environment and larval development, morphology, and behavior. Environmental experiences and other factors that impact survival and fitness ultimately shape long-term evolutionary patterns and legacies. Even phenotypically plastic traits and environmental responses are being recognized as important drivers of genetic legacies through genetic assimilation (Strathmann and others 1992; West-Eberhard 2003).

As we learn more about complex life-histories, it becomes clear that legacies are inexorably linked in the short term as well as the long term through ecology and evolution. Understanding the consequences and drivers of life-history patterns can therefore only be understood by considering all types of legacies and integrating legacies across the entire life cycle.

The legacies of Larry McEdward

As scientists, our ideas and research are a lasting legacy through our published work. Much like the phylogenetic legacies of organisms, our work is built on and influenced by the writings of and interactions with those who preceded us—specially teachers and mentors who helped us develop our scientific philosophies, skills and approaches to answering questions. Similarly, we impart a legacy on our colleagues, students, and those we train. We not only influence their research and scientific products through direct interactions and input, but we also create environments that can facilitate thought and the development of new ideas and approaches.

Larry has left many different types of legacies, not only through his research and publications, thoughts and ideas, but also through the time and devotion to his students, colleagues, friends, and family. Larry also inherited many important legacies from his colleagues and mentors, John Lawrence, Richard Strathmann, and Fu-Shiang Chia. These legacies not only affected his mentoring, teaching, and research, but were also passed on to his students and fellow colleagues. Larry trained 6 Masters and 7 Ph.D. students and influenced countless numbers of graduate and undergraduate students he taught at the University of Florida and at the Friday Harbor Laboratories. Larry's devotion to his family and friends, passions, and personal work-hard play-hard ethic, sense of humor and generous nature will provide lasting legacies for those who knew him, just as the development of the field of larval ecology and complex life-histories through his published science will have a legacy on the future scientific research.

We miss you Larry.

Larry McEdward's students

M.S. students	Ph.D. students
Ginny Eckert	Dan Janies
Elizabeth Niciu	Joan Herrera
Shannon McWeeney	Andreas Heyland*
Marianne Donhue	Cecelia Miles*
Adam Reitzel*	Ben Miner*
Jonathan Cowart*	

*Students in 2001.

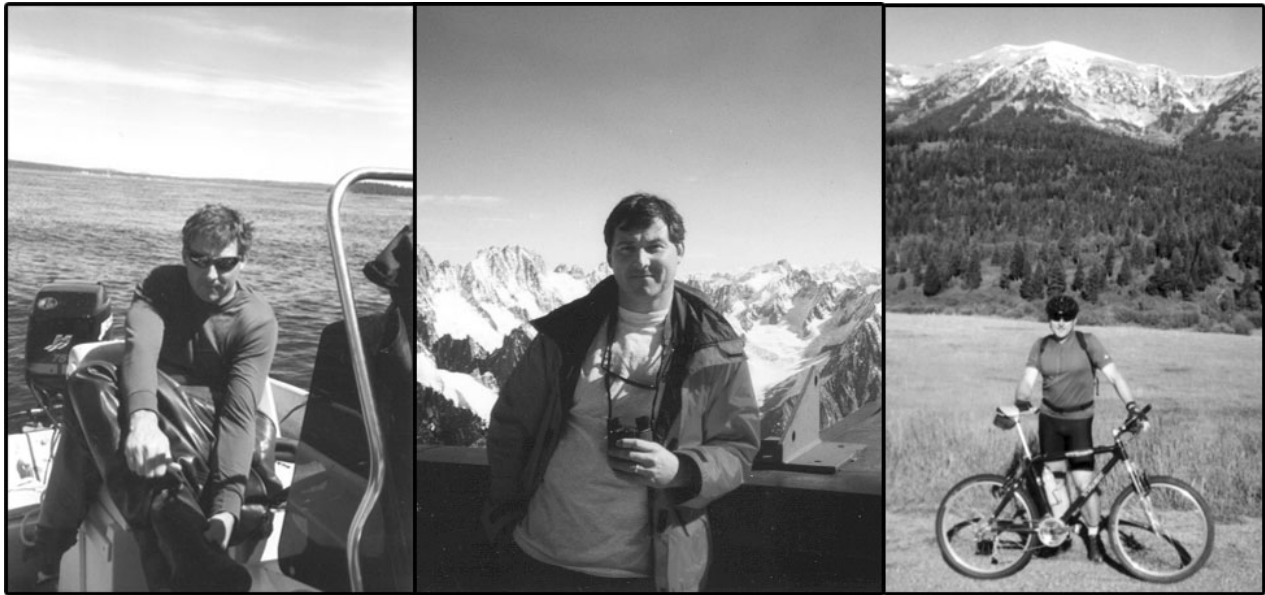


Fig. 2 Larry McEdward.

Larry McEdward's publications

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