

## **UC Davis**

### **UC Davis Previously Published Works**

**Title**

Ecological and Evolutionary Consequences of Linked Life-History Stages in the Sea

**Permalink**

<https://escholarship.org/uc/item/6d6269gr>

**Journal**

Current Biology, 21(18)

**ISSN**

0960-9822

**Authors**

Marshall, Dustin J  
Morgan, Steven G

**Publication Date**

2011-09-01

**DOI**

10.1016/j.cub.2011.08.022

Peer reviewed

# Ecological and Evolutionary Consequences of Linked Life-History Stages in the Sea Review

Dustin J. Marshall<sup>1,\*</sup> and Steven G. Morgan<sup>2</sup>

Naturalists and scientists have been captivated by the diversity of marine larval forms since they were discovered following the advent of the microscope. Because they often bear little resemblance to adults, larvae were identified initially as new life forms, classified into different groups based on the similarity of their body plans and given new names that are still with us today. The radically different body plans and lifestyles of marine larvae and adults have led most investigators historically to study the two phases of complex life cycles in isolation. More recently, important ecological insights have sprung from taking a holistic view of marine life cycles. Meanwhile, the evolutionary (phenotypic and genetic) links among life-history phases remain less appreciated. In this review, our objective is to evaluate the evolutionary links within marine life cycles, and explore their ecological and evolutionary consequences. We provide a brief overview of marine life histories, discuss the phenotypic and genetic links between the two phases of the life cycle and pose challenges to advance our understanding of the evolutionary constraints acting on marine life histories.

## Introduction

Marine life histories are remarkable. Some species release millions of tiny unfertilized eggs that spend months in the plankton (Figure 1) while others produce only few, carefully nurtured offspring that leave the parent only as fully formed juveniles. In contrast to terrestrial systems, life-history ‘strategies’ in the sea are often unconstrained by phylogeny — there can be as much variation in life-history strategies within genera, and sometimes even within a group of siblings, as there can be among entire phyla. For example, within a single egg mass from the sea slug *Alderia modesta*, some individuals can hatch as miniature versions of the adults while others hatch as free-swimming larvae [1]. Such variation has led to the view that marine life-history stages are evolutionarily independent of each other — across species, evolution in one life-history stage does not appear to necessitate evolution in another. These macroevolutionary patterns, however, may not reflect likely microevolutionary constraints imposed by phenotypic and genetic links across life history stages within individual species. Indeed, we suspect that within species, traits in one life-history stage are rarely able to evolve without consequences for another stage. We suggest that viewing marine life histories in a more holistic way, and recognizing the links among life-history stages, may provide important insights into their ecological and evolutionary consequences. We first introduce marine life histories and then highlight the links among different life-history stages, dealing first with phenotypic links and then genetic links among each stage.

## Ecology of Marine Life Histories

The vast majority of marine species develop as planktonic larvae regardless of the habitats of adults. We will focus here on species that are sessile or sedentary as adults because their benthic lifestyles differ most dramatically from their planktonic lives as larvae. Survival depends on surviving critical junctures in these complex life cycles, beginning with entering the water column and ending with returning to the bottom (Figure 2). Diverse suites of traits enable tiny larvae (mostly <1 mm) to complete these life cycles against seemingly overwhelming odds [2].

The transition from the benthos to the plankton occurs by spawning or hatching. Many, if not most, species reproduce via the ancestral reproductive strategy of spawning gametes into the water column, though some release externally fertilized gametes that remain on the benthos. It was once assumed that the success of sperm fertilizing eggs would be low, especially in strong, turbulent flow, but evidence has been mixed: some field studies suggest that up to 95% of eggs can be fertilized (e.g., [3,4]) while others have recorded very low rates of fertilization [5]. At an individual level, the fertilization success of some will be limited by access to gametes of the opposite sex, but in others, success will be limited by the presence of too many sperm [6]. Some species communicate via pheromones to coordinate spawning events [7], while many others rely on environmental cycles to synchronize spawning, with the level of synchrony varying both within and among species [8,9]. In species with internal fertilization, the resulting embryos are either brooded by parents or released in protective capsules [9,10]. Swimming larvae may hatch synchronously relative to environmental cycles at times that may maximize survival of offspring. For example, many species of crabs and coral reef fishes release larvae during spring, ebb tides under the cover of darkness, maximizing transport away from high densities of predators before dawn [11–13].

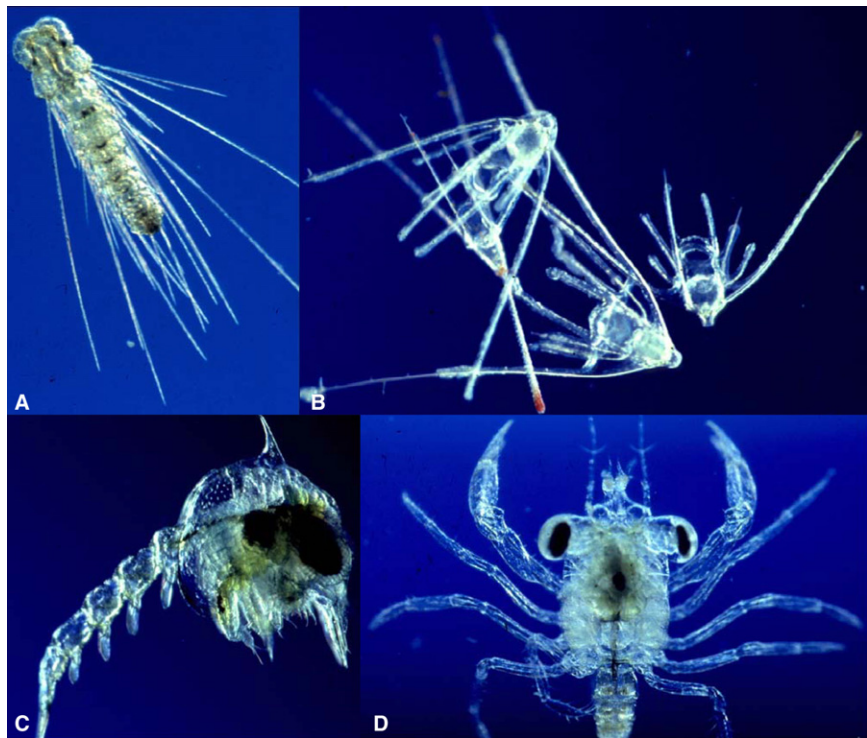
Larvae suffer mortality from a variety of sources. Compared to their much larger parents, tiny planktonic larvae are exposed to a wide array of predators as they develop in the plankton and re-enter adult habitats. Consequently, predation rates are probably high on larvae, and many types of morphological, behavioral and chemical defenses are apparent [2]. The nutritional sources and time spent developing in the plankton differ widely among species, but they fall into two types: planktotrophic larvae capture zooplankton, phytoplankton or bacteria, and when feeding in oligotrophic waters, are prone to starvation [13]; by contrast, lecithotrophic larvae are provisioned with yolk, thus reducing the risk of starvation. The two different larval feeding modes have important life history consequences: planktotrophs are energetically cheaper to produce, but also spend more time in the dangerous plankton relative to lecithotrophs [14]. It was first proposed that, because of their long larval periods, planktotrophs are more dispersed, resulting in expansive geographic ranges, reduced local adaptation and lower extinction and speciation rates [15–17]. However, evidence for macroevolutionary consequences of larval durations has been mixed, perhaps because not all larvae are passively dispersed by currents [18].

<sup>1</sup>School of Biological Sciences, University of Queensland, 4072, Australia. <sup>2</sup>Bodega Marine Laboratory, Department of Environmental Science and Policy University of California Davis, USA.

\*E-mail: d.marshall1@uq.edu.au

Figure 1. Diversity of marine larvae.

(A) Late-stage larva of a polychaete worm (setiger); (B) three brittlestar larvae (ophioplutei); (C) crab larva (zoea); and (D) crab post-larva (megalopa). (C,D) Photographs courtesy of Peter Parks.



It was long held that tiny larvae were poor swimmers and pushed offshore by currents, and most were prevented from recruiting back into the adult population [14,19,20]. However, mounting evidence over the last century revealed that some larvae can exert considerable control over the distance and direction traveled [21]. Larvae of many coastal species migrate offshore before returning to settle in adult habitats, and in doing so exploit persistent circulation patterns. For example, stratified currents that flow in opposing directions at different depths are used as a 'conveyor belt' to regulate upstream-downstream transport in estuaries and offshore-onshore and alongshore transport in coastal waters [22,23].

When settling down, the larvae of sessile marine invertebrates face an enormous challenge — given their limited sensory facilities, they must choose a site to which they will be attached for the rest of their lives and that supports life. Multiple cues guide larvae to settle from the water column before searching the substrate for an appropriate spot, ranging from tactile and hydrodynamic cues to chemical cues from complex bacterial communities growing on highly specific surfaces [24]. Interestingly, individual variation in settlement preferences among siblings may diversify the range of habitats that are colonized, thereby increasing the chances of survival [25,26]. Overall then, adult and larval phases are intimately coupled through mechanisms that foster successful completion of the life cycle.

There has been a long history of investigators emphasizing the importance of either the larval or the adult phase of the life cycle in regulating marine population size [27]. We now know that populations can be regulated during either phase of the life cycle, and that the relative importance of planktonic and benthic processes varies in time and space. Conditions that frequently favor the completion of the larval phase result in abundant recruitment, saturation of available settlement sites and intense post-settlement interactions resulting in high mortality, especially of recent settlers [28]. For example, barnacle settlement on the west coast of North America can carpet all available surfaces in recruits and adults can form dense, 'hummocked' aggregations where each individual elongates to access the water column above its neighbor. Conversely, frequent and high mortality during the larval phase results in few recruits, abundant open space, weak species interactions and possibly lower post-settlement mortality. Therefore, both phases of the life cycle must be studied to determine the weak link(s) in the life cycle, and the conditions that are responsible for its failure. Such a holistic view of the ecology of marine life-

history stages is now well-accepted and has led to important changes in the way we view and manage marine populations.

#### Phenotypic Links between Marine Life-History Stages

Although demographic, numerical links among life-history stages have been studied for some time, the study of phenotypic links is more recent. The phenotype of a settling larva in fact appears to strongly affect the phenotype of the metamorphosed juvenile [29]. The strong phenotypic link across metamorphosis is surprising at first glance, given the associated changes in body plan, habitat and even mode of feeding in some species. Upon further consideration, however, it is clear the basic composition of the individual does not reset completely [30]. Consequently, any condition that modifies the phenotype of a larva will almost inevitably influence the phenotype of the metamorph, including variation in energy reserves due to variation in larval nutrition, larval duration and maternal provisioning, as well as physiological stress and maternal experience [29].

These 'carry-over' or 'latent' effects (*sensu* [29]) affect both the performance of metamorphs and the dynamics of adult populations. Although over 50 years ago pioneers of marine ecology had already speculated about intraspecific variation in larval phenotype affecting population dynamics [30,31], most ecological considerations of marine life histories have neglected this variation. Early theoretical considerations of the population dynamics of marine species with complex life cycles assumed that all larvae have the same capacity to survive and reproduce. Recent work, however, has shown that variation in larval phenotype can be more important than variation in larval supply in regulating marine populations. For example, populations founded by a single high-quality individual can have reproductive outputs that are equivalent to populations founded by 30 low-quality individuals [32].

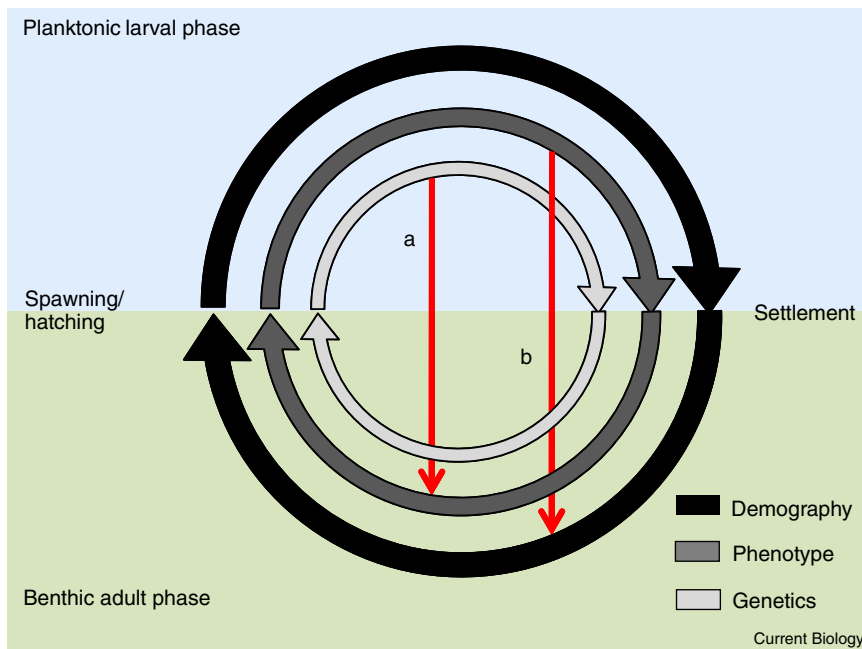


Figure 2. Generalized life cycle of a marine organism.

The black cycle represents demographic links among life-history stages, the grey cycle represents phenotypic links and the light grey cycle represents genetic correlations. While the demographic links among life-history stages are well recognized, the genetic (genetic correlations) and phenotypic (maternal effects and latent effects) links are far less understood. The thin red arrows indicate how different components (demography, phenotype and genetics) are linked. Arrow 'a' indicates that genetic factors in the larval phase can affect phenotype in the adult phase, and arrow 'b' indicates that larval phenotype can affect adult demography.

A consequence of phenotypic links among stages is that separated populations can be linked phenotypically (Figure 2). Such links among populations arise because larvae dispersing from one population to another bear a signature phenotype that is partly a product of their natal environment. Exposure to different environmental conditions can lead to variation in larval phenotypes via direct effects on larvae and via maternal effects [33]. The mean phenotype of a population will, therefore, not only be a product of the local environment, as is traditionally thought [18], but also of conditions in other populations that are linked through dispersal. In other words, the mean phenotype of any one population may be more a product of the mean environment of the metapopulation than previously realized. Given the potential for long-distance larval dispersal, these effects could manifest far away, making management of marine populations more difficult. For example, marine protected areas could incidentally foster the evolution of less dispersive phenotypes, reducing replenishment of fished populations [34].

Phenotypic links between mother and offspring also can have lasting effects on subsequent generations. For example, exposure of mothers to heavy metals can induce phenotypic plasticity in their offspring, increasing the resistance of offspring to toxicants and predation but reducing resistance to salinity stress and intraspecific competition [35]. In terrestrial systems, such maternal effects have been shown to persist for up to three generations [36] but similar studies are lacking in marine systems. Overall, the phenotype and performance of a population are unlikely to be a simple product of local conditions; rather both will be influenced by conditions in previous generations as well as potentially distant populations.

Phenotypic links among life-history stages could either increase or decrease connectivity among populations [37]. Effective population connectivity requires survival and reproduction after dispersal, so population connectivity will decrease when dispersal is costly [38,39]. Phenotypic links among life-history stages can increase the cost of dispersal in two ways: first, when duration of the larval stage affects

subsequent performance, individuals that travel for longer periods will survive and reproduce less due to the energetic costs of dispersal [29]. Second, when larvae bear a phenotype that is well suited to local conditions, movement to a new population with

different conditions will reduce their chances of surviving and reproducing even when their phenotype is plastic [33]. Such phenotype–environment mismatches may be especially prevalent in the sea because of the potential for long-distance larval transport. This also has some interesting implications for how we view anthropogenic impacts. For example, local pollution may not only decrease the abundance of individuals within that population, it could also generate phenotype–environment mismatches, thereby reducing connectivity and the subsequent recovery.

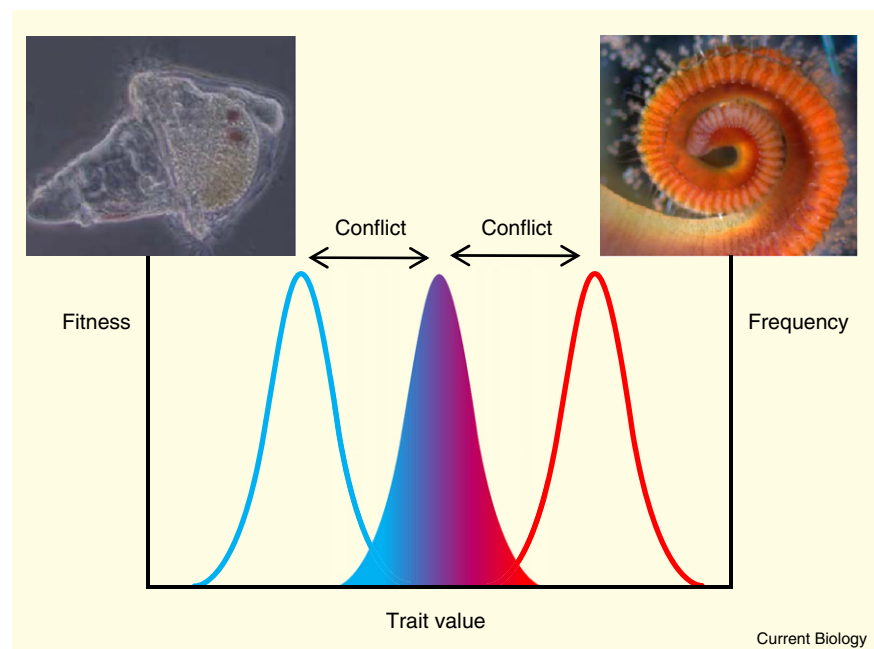
#### Microevolutionary Consequences of Linked Marine Life Histories

While different life-history stages are increasingly viewed as ecologically linked, the evolution of larval and adult traits are still largely viewed and studied as distinct from each other. This view is based largely on macroevolutionary patterns of marine invertebrate life-history strategies. When one examines the vast diversity of marine life histories, larval size, form and trophic mode can vary enormously within even a single genus, while the adults of each species can be almost indistinguishable. Instances where larval or adult traits vary independently among species strongly suggest that evolution within one life-history stage does not necessitate evolution in another [40]. Such decoupling between life-history stages is not restricted to larval form but can also extend to physiology. For example, the larvae of some deep-sea invertebrates cannot tolerate the cooler temperatures that their parents thrive in, and instead require warmer temperatures that would kill their parents [41]. This physiological flexibility suggests that larvae and adults can indeed do very different things. More generally, such patterns have led some to suggest that complex life histories represent an adaptation that allows the expression of the optimal phenotype in each life-history stage, an idea known as the 'adaptive decoupling hypothesis' [42,43]. According to this hypothesis, metamorphosis acts like a 'firewall': the evolutionary pressures and constraints that act on one life-history stage cannot influence the other [42]. We agree that there are



Figure 3. Potential evolutionary tug-of-war between selection on shared larval and adult traits.

The black line represents the distribution of a trait within a population, the red and blue curves represent the optimum value of that trait for the larval and adult phases, respectively. Most considerations of marine life cycles assume either that trait correlations do not span the two phases of the life cycle or that the optima for different life-history stages are identical, although recent evidence suggests that neither condition holds. Photographs show the tubeworm *Galeolaria caespitosa*, as trochophore larva (left) and a spawning mother (right), courtesy of Richard Allen and Laura McLeod.



many instances where macroevolutionary patterns suggest that larvae and adults can overcome evolutionary constraints over geological timescales. But, for several reasons, we are skeptical as to whether contemporary marine life histories are adaptively decoupled.

While marine life-histories have repeatedly evolved to overcome constraints, these macroevolutionary patterns may not always reveal the contemporary role of constraints across the life history. For example, adult morphology in *Drosophila* varies between species, but the larvae of most species are indistinguishable, suggesting that, at a macroevolutionary level, adult morphology is free to evolve independently of larval morphology [42]. Nevertheless, within species of *Drosophila*, strong correlations have been identified for a range of life-history traits, suggesting that each life-history stage places constraints on the other [44], thereby constraining microevolutionary change. Therefore, the degree to which contemporary marine life histories for any one species are evolutionarily decoupled remains largely unknown, but we suspect that life-history stages are actually less free to vary independently than is currently appreciated.

Despite their major differences in habitat and form, different life-history stages share the same genome, the same tissues and the same body, all of which must introduce some constraints on evolution [45]. At the extreme, one stage may simply be a co-evolutionary by-product of evolution in another stage. However, it is more likely that evolutionary constraints preclude (or at least retard) either life-history stage from reaching its evolutionary optimum because selection is likely to act on both (Figure 3). If such constraints exist, then it has important consequences for the way we view the ecology and evolution of marine organisms with complex life histories. To illustrate this, we will use one of the simplest, most powerful tools in evolutionary biology — the multivariate breeders' equation:

$$\Delta z_1 = (G_{1,1} \times \beta_1) + (G_{1,2} \times \beta_2),$$

where  $z_1$  represents the change in the value of trait 1 from one generation to the next,  $G_{1,1}$  is the additive genetic variance in the trait one,  $\beta_1$  is selection on trait 1,  $G_{1,2}$  is the genetic covariance between traits one and two and  $\beta_2$  is selection on trait 2. The multivariate breeders' equation predicts that the amount

of change in a trait from one generation to the next is determined by the magnitude of selection and the level of heritable genetic (co)variance. Adaptive evolutionary change cannot occur in the absence of selection or heritable genetic variance in the dimension in which selection acts [46]. While this equation has been with us for over 30 years, it continues to provide valuable insights into the evolution of multiple traits [47]. The multivariate breeder's equation is particularly valuable because its components are directly estimated from relatively simple empirical studies, yet marine biologists, for the most part, have not taken advantage of this powerful approach. Based on this equation, we can explore possible constraints on marine organisms with complex life histories.

Let us begin with a consideration of selection. The phenotypic links among life-history stages complicate our view of selection in marine organisms. Because a phenotype can be expressed in more than one life-history stage, the net selection on that phenotype will be a product of selection on multiple stages (Figure 4). Thus, phenotypes that carry a selective advantage in one life-history stage could also suffer a selective disadvantage in a subsequent life-history stage, a kind of internal trade-off. Consequently, the product of such conflicting selection pressures may be no net selection on the trait of interest, leaving that trait as an awkward compromise that balances the two opposing sources of selection. Although the idea that traits that pervade the life history can be under conflicting selection pressures is not new [48], it has rarely been considered in marine organisms [12,49]. Considerations of conflicting (or even complementary) selection pressures across the life history of a marine organism are usually restricted to offspring size [50] — a trait that most obviously crosses multiple life-history stages. Even then, a genuinely longitudinal study tracking an individual of known offspring size across the entire life history has yet to be done; nor has a study brought to bear the analytical approaches best suited for integrating selection across the entire life history [51]. Metabolic rate, stress tolerance and other physiological processes are also likely

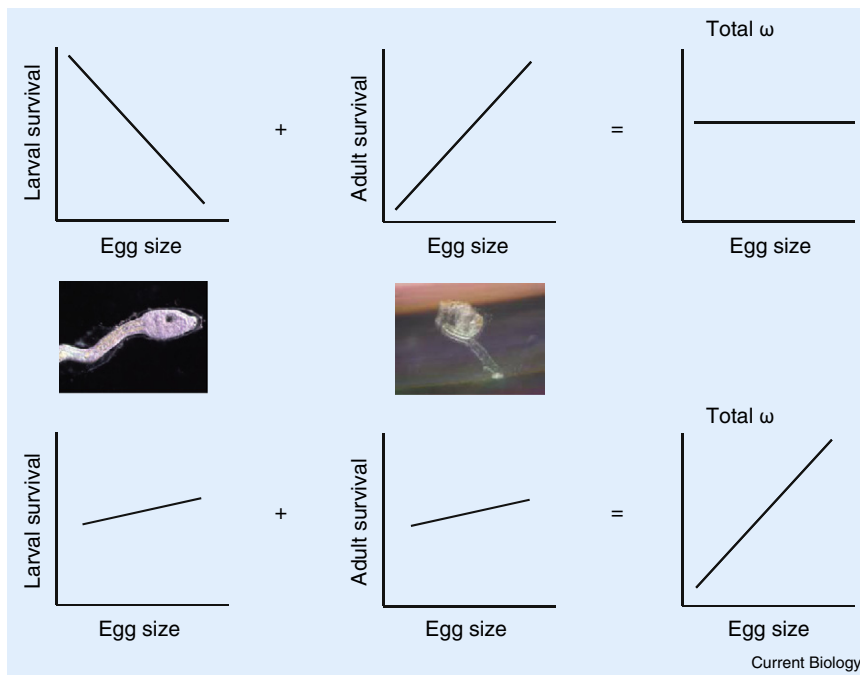


Figure 4. Conflicting and complementary selection pressures across the life cycle.

The top three panels show an idealized example of conflicting selection pressures where positive selection on egg size in one life-history stage is cancelled out by negative selection on egg size in another life-history stage, resulting in no net selection on egg size (not relationship between egg size and total fitness, shown as  $\omega$ ). In this case, the selection pressures on egg size would be overestimated by focusing on life-history stage alone. The bottom panel shows an example of complementary selection pressures where weakly positive selection on egg size occurs in both life-history stages, resulting in strong selection for increases in egg size. In this case, focusing on one life-history stage in isolation would lead to an underestimation of net selection on egg size. No study has yet followed selection on a trait across the entire life-history of a marine invertebrate. Photographs show an ascidian tadpole larva and post-metamorphic settler, courtesy of David Aguirre-Davies.

to be linked among stages increasing the potential for conflicting selection pressures, although they have not yet been explored in marine organisms. Viewing the evolution of traits through the lens of sexual conflict has led to important progress in species with sexual reproduction [52]; similar gains may be possible if we incorporate potential conflict among life-history stages into our view of evolution in species with complex life cycles.

Let us now consider the other half of the breeders' equation: genetic variation. If there is a heritable genetic correlation between two traits, then selection on one trait will result in a correlated response to selection on the other trait, despite no observable phenotypic link between the two traits [53]. To illustrate this point, if we re-examine the multivariate breeders' equation and imagine trait 1 ( $z_1$ ) is a larval trait and trait 2 is an adult trait, when selection on the adult trait occurs ( $\beta_2$ ) because of genetic covariance between the adult trait and the larval trait ( $G_{1,2}$ ), the larval trait will evolve despite no direct selection acting on the larval trait (i.e.  $\beta_1 = 0$ ). The situation is even more complicated when both traits are linked to fitness: selection will not proceed as expected, and depending on the nature of the genetic correlation between the traits, evolution may not take place at all, despite strong selection for change in the value of one or both traits [46]. Importantly, the multivariate breeders' equation shows that genetic correlations can constrain evolution even when there appears to be abundant genetic variance in each trait separately (Figure 5). Viewing genetic variation in a univariate context may lead to misleading conclusions about the strength of selection on a trait or its potential to evolve [53,54]. We suspect that such correlations are common, though the degree to which traits in different life-history stages are genetically correlated in marine organisms is almost completely unknown.

There is some evidence that life-history stages are genetically coupled. Genetic correlations persist across the metamorphic boundary in terrestrial and freshwater organisms

[44,55,56], but in marine organisms, evidence is limited and mixed. In a polychaete worm, an oyster and a fish, strong genetic correlations exist across metamorphosis [57–59], but in a clam, no correlation was detected [54]. In addition to likely correlations between physiological processes among life-history stages, some adult structures are derived from larval skeletal or tissue components in several marine groups, suggesting that some morphological traits could persist across metamorphosis [60,61]. Finally, molecular studies in marine invertebrates suggest that gene transcription can link life-history stages; the expression of some genes continues across the metamorphic boundary while the expression of other genes does not [62–64]. Whether these molecular studies reflect additive genetic variance remains unclear, and later we discuss how molecular studies can inform our view of constraints across life-history stages.

Evolution in one life-history stage can be constrained by another life-history stage both through selection and genetic (co)variance, and we reiterate earlier calls for a whole life cycle view of evolution in the sea [57,65]. Larval forms will almost certainly be a product of selection in the larval environment, but they are also likely to be a product of indirect selection on the adult form via shared traits and genetically correlated traits. An evolutionary view of marine life histories that recognizes the links among life stages is likely to yield similar advances to those gained by ecologists when they recognized the ecological links among stages. In the absence of such studies, we wonder how many viable adult phenotypes are precluded because evolutionary constraints render these same phenotypes unviable as larvae, and how many larval forms are simply products of constraints or selection on the adult [66,67]. In the absence of such studies, we would caution against the interpretation of any distribution of trait values as solely a product of selection in one particular life-history stage — other, seemingly unrelated traits in other life-history stages could also have an influence [49,59].

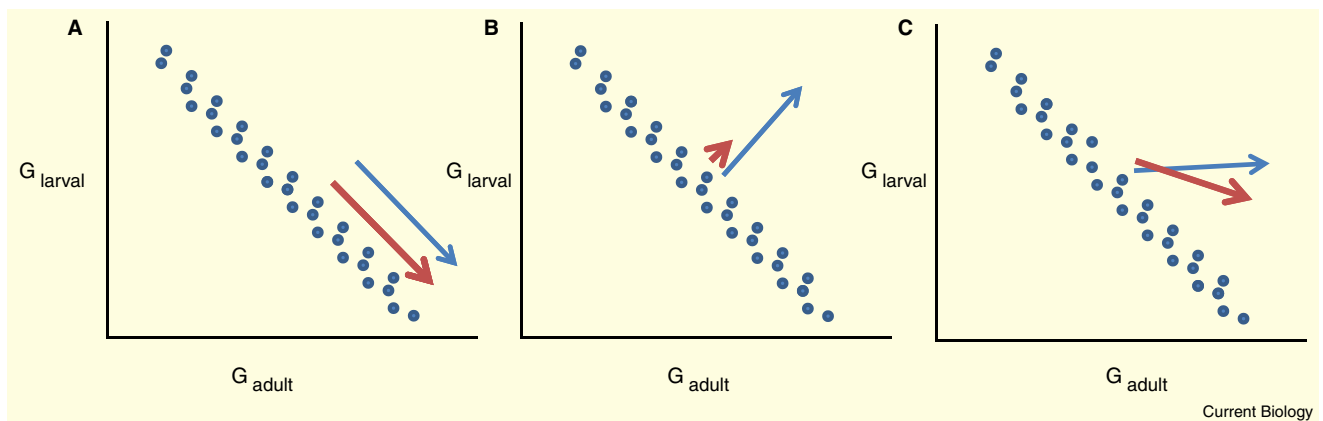


Figure 5. Genetic correlations can constrain the evolution of life histories in the sea.

In all three panels, the dots reflect the additive genetic trait value for traits in two life-history stages (shown as  $G_{larval}$  and  $G_{adult}$  where each dot represents one individual). The blue arrows show the direction and magnitude of selection acting on the mean of the population and the red arrows show the direction and magnitude of the response to selection. In all cases, the magnitude of selection is identical but the response to selection depends on the degree of alignment between selection and genetic variation. (A) Unimpeded evolution when selection acts in the same direction as most of genetic variation; (B) little evolutionary response when selection acts orthogonally to the dimension in which most of the genetic variation occurs; (C) the response to selection is biased towards the path of least genetic resistance (red arrow) when selection is not aligned with the dimension in which genetic variation lies.

### Future Challenges and Directions

The degree to which marine life histories constrain evolution remains unclear because appropriate studies are sorely lacking. We propose that three well-established evolutionary approaches should be applied to address this question [53]: first, formal estimates of selection on traits that are expressed in multiple life-history stages (offspring size, metabolism, etc.) are needed to determine the prevalence of conflicting selection pressures across life-history stages (Figure 3) [68,69]. Recent reviews have highlighted that focusing alone on linear selection — i.e. a linear relationship between the traits of interest and fitness — can lead to an incomplete view of selection [69]. Instead, estimates of selection that consider the combination of two or more traits simultaneously known as correlational selection, and estimates of selection that include curvilinear forms of selection, known as quadratic selection, are necessary in order to more fully describe selection on a trait or suite of traits. Correlational selection in particular would seem relevant to studies of marine life histories if different trait combinations have different effects on fitness [49]. Formal selection analyses directly equate statistical estimates of the relationship between traits and fitness to concepts about the strength, direction and nature of selection on those traits [66]. This powerful approach has proven invaluable for understanding evolution when used with caution [51,70], but generalizations about the strength and prevalence of selection are not yet possible in marine systems (but see [49,71,72]). Second, quantitative genetics studies that estimate additive genetic correlations across the metamorphic boundary will provide estimates for the potential for evolution and highlight any genetic constraints acting on marine life histories (Figure 5) [43,46,66]. Marine organisms with external fertilization are particularly well suited to such studies because eggs and sperm can be divided and cross-fertilized in combination. Hence, additive genetic variation can be estimated without the more complicated breeding designs and analyses required for species with internal fertilization [57,73,74]. Our call for such studies echoes those made

during the last 30 years [45,57,65], yet such studies still remain rare. The third approach is most difficult and informative; experimental evolution studies reveal the consequences of selection on one life-history stage for evolution in another [45,55]. To our knowledge, only Miles and Wayne [75] have examined the consequences of selection on one life-history stage for another stage in a marine invertebrate. By selecting for increased egg size in the tube-worm *Hydroides elegans*, the transition from male to female function occurred sooner, demonstrating how selection on one life-history stage can induce correlated responses in seemingly unrelated traits in another stage [75]; we cannot think of a more compelling illustration of why an integrated view of life-history evolution is required.

Future studies should, where possible, integrate molecular approaches with quantitative genetics. We believe that quantitative genetics is essential. In the absence of quantitative genetics approaches, the heritability of any molecular variation that is observed remains unclear, and yet it is this heritability of genetic (co)variance that will determine the response to selection over multiple generations [76]. Fellous and Lazzaro [77] recently provided an excellent example of how molecular and quantitative genetic approaches can be combined to yield powerful insights into life-history constraints at a mechanistic level. By combining a breeding design with measurements of gene expression in *Drosophila*, they identified non-additive genetic correlations between the expression of an antimicrobial peptide in the larval phase and the adult stage. Such insights would be impossible if either approach was used in isolation, and we encourage further studies that integrate the two.

The interaction between ecology and evolution can be particularly complicated in marine organisms with complex life histories. The potentially high mortality rates that larvae are believed to suffer while in the plankton represent a major selection pressure. While some of this mortality will be random with respect to larval phenotypes, much of it will not be [2], shifting the distribution of phenotypes that leave

the plankton from the original distribution that entered the plankton. In some instances, this selection can counteract other ecological effects. For example, recruits derived from oligotrophic, oceanic waters can survive better than recruits from more productive inshore waters [39], but we would have expected the opposite based on the familiar physiological effects of larval nutrition [78]. Apparently, selection on high-performing phenotypes was stronger in the oceanic cohorts, lifting the mean performance of individuals from these sites. This finding raises an important caveat that remains to be addressed when investigating the phenotypic links between life-history stages [29]: it is difficult to discriminate between the effects of manipulating the larval phenotype (to which any differences in performance are usually ascribed [29]), and the effects of selection when the larval treatment induces mortality, because this mortality is unlikely to be completely random with respect to larval traits. Thus, we may be confusing selection for carry-over effects in some instances and future studies should seek to disentangle these two effects. In the field, selection pressures among life-history stages may differ greatly when larvae cross into new environments. Selective sweeps in the plankton could dramatically change the distribution of settling phenotypes [79] (but see [80]), changing the evolutionary trajectory of adult populations even where adult environments are fairly stable.

Gamete and larval stages of marine organisms have long been considered to be the most sensitive and therefore the weakest link when considering the impacts of environmental stress. Consequently, studies on the impacts of heavy metal pollution, ocean acidification and effluent discharge usually focus on early life-history stages [81,82]. These studies usually collect gametes or larvae from 'naïve' mothers that have not been exposed to the environmental stress themselves [82]. It appears increasingly that mothers can modify the phenotype of their offspring in response to environmental stressors generally, and in marine systems in particular [35], thereby reducing the impact of the stress while increasing the susceptibility to other stresses in the second generation via transgenerational plasticity [83]. Therefore, whenever mothers and offspring are likely to experience the same stress, such as when the duration of stress spans generations or populations (e.g. climate change effects), using naïve mothers may not accurately estimate the impacts of that stress. Future studies of the impacts of environmental stress on gametes and larvae should incorporate the role of transgenerational plasticity to avoid misleading conclusions resulting from ignoring maternal effects on larval phenotypes [84].

An understanding of how evolutionary constraints affect form, physiology and resilience across life histories is crucial to a more complete understanding of the ecology of marine organisms. For example, species ranges may be the product of direct selection on the adult stage and indirect selection imposed by the larval stage. The ability of marine organisms to adapt to change will be limited by the constraints among stages, although the strength and nature of these constraints remain unknown [85]. Barriers to connectivity may be evolutionary as well as ecological [33], but their importance also remains unknown. We have made tremendous progress in understanding the ecology of diverse life histories in the sea during the last century, and the time is ripe to advance our understanding of the evolutionary links within these fascinating life histories.

## Acknowledgements

We thank K. McGuigan, P.J. Krug and D. Ortiz Barrientos and two anonymous reviewers for very helpful and insightful comments on earlier versions of this manuscript, and S.F. Chenoweth and M.W. Blows for helpful discussions about selection and genetic (co) variance. The writing of this manuscript would not have been possible without the help of friends and strangers in the wake of the 2011 floods in Brisbane. D.J.M. was supported by grants from the Australian Research Council, and S.G.M. was supported a grant from the National Science Foundation (OCE-0927196).

## References

1. Krug, P.J. (1998). Poecilogony in an estuarine opisthobranch: planktotrophy, lecithotrophy, and mixed clutches in a population of the ascoglossan *Alderia modesta*. *Mar. Biol.* 132, 483–494.
2. Morgan, S.G. (1995). Life and death in the plankton: larval mortality and adaptation. In *Ecology of Marine Invertebrate Larvae*, L. McEdward, ed. (Boca Raton: CRC Press), pp. 279–321.
3. Pennington, J.T. (1985). The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation and synchronous spawning. *Biol. Bull.* 169, 417–430.
4. Peterson, C.W., Warner, R.R., Cohen, S., Hess, H.C., and Sewell, A.T. (1992). Variation in pelagic fertilization success; implications for production estimates, mate choice, and the spatial and temporal distribution of spawning. *Ecology* 73, 391–401.
5. Levitan, D.R. (1995). The ecology of fertilization in free-spawning invertebrates. In *Ecology of Marine Invertebrate Larvae*, L.R. McEdward, ed. (Boca Raton: CRC Press, Inc.), pp. 124–152.
6. Franke, E.S., Babcock, R.C., and Styan, C.A. (2002). Sexual conflict and polyspermy under sperm-limited conditions: In situ evidence from field simulations with the free-spawning marine echinoid *Evechinus chloroticus*. *Am. Nat.* 160, 485–496.
7. Hamel, J., and Mercier, A. (1997). Evidence of chemical communication during gametogenesis of holothuroids. *Ecology* 77, 1600–1616.
8. Giese, A.C., and Kanatani, H. (1987). Maturation and spawning. In *Reproduction of Marine Invertebrates, Vol. 9*, A.C. Giese, J.S. Pearse, and V.B. Pearse, eds. (Palo Alto: Blackwell Scientific), pp. 251–329.
9. Morgan, S.G. (1995). The timing of larval release. In *Ecology of Marine Invertebrate Larvae*, L.R. McEdward, ed. (Boca Raton: CRC Press), pp. 157–191.
10. Barlow, G.W. (1981). Patterns of parental investment, dispersal and size among coral-reef fishes. *Env. Biol. Fishes* 6, 65–85.
11. Morgan, S.G., and Christy, J.H. (1995). Adaptive significance of the timing of larval release by crabs. *Am. Nat.* 145, 457–479.
12. Morgan, S.G., and Anastasia, J.R. (2008). Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *Proc. Natl. Acad. Sci. USA* 105, 222–227.
13. Olson, R.R., and Olson, M.H. (1989). Food limitation of planktotrophic marine larvae: does it control recruitment success? *Annu. Rev. Ecol. Syst.* 20, 225–247.
14. Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1–45.
15. Scheltema, R.S. (1975). Relationship of larval dispersal, gene-flow and natural selection to geographic variation of benthic invertebrates in estuaries and along shorelines. In *Estuarine Research*, L.E. Crosonin, ed. (New York: Academic Press), pp. 372–391.
16. Crisp, D.J. (1978). Genetic consequences of different reproductive strategies in marine invertebrates. In *Marine Organisms Genetics, Ecology and Evolution*, B. Battaglia and J. Beardmore, eds. (New York: Plenum Press), p. 257.
17. Jablonski, D., and Lutz, R.A. (1983). Larval ecology of marine benthic invertebrates: paleontological implications. *Biol. Rev.* 58, 21–89.
18. Sanford, E.D., and Kelly, M.W. (2011). Local adaptation in marine invertebrates. *Annu. Rev. Mar. Sci.* 3, 509–535.
19. Roughgarden, J., Gaines, S., and Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science* 241, 1460–1466.
20. Wolanski, E., and Hamner, W.M. (1988). Topographically controlled fronts in the ocean and their biological influence. *Science* 241, 177–181.
21. Swearer, S.E., Shima, J.S., Hellberg, M.E., Thorrold, S.R., Jones, G.P., Robertson, D.R., Morgan, S.G., Selkoe, K.A., Ruiz, G.M., et al. (2002). Evidence of self-recruitment in demersal marine populations. *Bull. Mar. Sci.* 70, 251–271.
22. Queiroga, H., and Blanton, J. (2005). Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv. Mar. Biol.* 47, 107–214.
23. Morgan, S.G., Fisher, J.L., Miller, S.H., McAfee, S.T., and Largier, J.L. (2009). Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* 90, 3489–3502.
24. Steinberg, P.D., De Nys, R., and Kjelleberg, S. (2002). Chemical cues for surface colonization. *J. Chem. Ecol.* 28, 1935–1951.
25. Raimondi, P.T., and Keough, M.J. (1990). Behavioural variability in marine larvae. *Aust. J. Ecol.* 15, 427–437.



26. Toonen, R.J., and Pawlik, J.R. (2001). Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* 55, 2439–2454.
27. Young, C.M. (1990). Larval ecology of marine invertebrates: a sesquicentennial history. *Ophelia* 32, 1–48.
28. Underwood, A.J., and Keough, M.J. (2001). Supply-side ecology: the nature and consequences of variations in recruitment of intertidal organisms. In *Marine Community Ecology*, M.D. Bertness, S.D. Gaines, and M.E. Hay, eds. (Sunderland: Sinauer), pp. 183–200.
29. Pechenik, J.A. (2006). Larval experience and latent effects - metamorphosis is not a new beginning. *Integr. Comp. Biol.* 46, 323–333.
30. Barnes, H. (1953). Size variations in the cyprids of some common barnacles. *J. Mar. Biol. Assoc. UK* 32, 297–304.
31. Connell, J.H. (1961). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31, 61–104.
32. Burgess, S.C., and Marshall, D.J. (2011). Are numbers enough? Colonizer phenotype and abundance interact to affect population dynamics. *J. An. Ecol.* 80, 681–687.
33. Marshall, D.J., Monro, K., Bode, M., Keough, M.J., and Swearer, S. (2010). Phenotype-environment mismatches reduce connectivity in the sea. *Ecol. Lett.* 13, 128–140.
34. Baskett, M.L., Levin, S.A., Gaines, S.D., and Dushoff, J. (2005). Marine reserve design and the evolution of size at maturation in harvested fish. *Ecol. Appl.* 15, 882–901.
35. Moran, D.T., Dias, G.M., and Marshall, D.J. (2010). Associated costs and benefits of a defended phenotype across multiple environments. *Func. Ecol.* 24, 1299–1305.
36. Benton, T.G., Plaistow, S.J., Beckerman, A.P., Lapsley, C.T., and Littlejohns, S. (2005). Changes in maternal investment in eggs can affect population dynamics. *Proc. R. Soc. B Biol. Sci.* 272, 1351–1356.
37. Nosil, P., Vines, T.H., and Funk, D.J. (2005). Perspective: Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution* 59, 705–719.
38. Pineda, J., Hare, J.A., and Sponaugle, S. (2007). Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20, 22–39.
39. Hamilton, S.L., Regetz, J., and Warner, R.R. (2008). Postsettlement survival linked to larval life in a marine fish. *Proc. Natl. Acad. Sci. USA* 105, 1561–1566.
40. Wray, G.A. (1992). The evolution of larval morphology during the post-Paleozoic radiation of Echinoids. *Paleobiology* 18, 258–287.
41. Hamasaki, H.K., Nakajima, K., Tsuchida, S., Kado, R., and Kitada, S. (2010). Number and duration of zoeal stages of the hydrothermal vent crab *Gandalfus yunohana* from laboratory reared specimens. *J. Crust. Biol.* 30, 236–240.
42. Moran, N.A. (1994). Adaptation and constraint in the complex life-cycles of animals. *Annu. Rev. Ecol. Syst.* 25, 573–600.
43. Ebenman, B. (1992). Evolution in organisms that change their niche during the life cycle. *Am. Nat.* 139, 990–1021.
44. Chippindale, A.K., Hoang, D.T., Service, P.M., and Rose, M.R. (1994). The evolution of development in *Drosophila melanogaster* selected for postponed senescence. *Evolution* 48, 1880–1899.
45. Wray, G.A. (1995). Evolution of larvae and developmental modes. In *Ecology of Marine Invertebrate Larvae*, L.R. McEdward, ed. (Boca Raton: CRC), pp. 413–448.
46. Blows, M.W., and Hoffmann, A.A. (2005). A reassessment of genetic limits to evolutionary change. *Ecology* 86, 1371–1384.
47. Hoffman, A.A., and Sgro, C.M. (2010). Climate change and evolutionary adaptation. *Nature* 470, 479–485.
48. Schluter, D., Price, T.D., and Rowe, L. (1991). Conflicting selection pressures and life-history trade-offs. *Proc. R. Soc. Lond. B Biol. Sci.* 246, 11–17.
49. Crean, A.J., Monro, K., and Marshall, D.J. Fitness consequences of larval traits persist across the metamorphic boundary. *Evolution* (in press.)
50. Marshall, D.J., Allen, R.M., and Crean, A.J. (2008). The ecological and evolutionary importance of maternal effects in the sea. *Oceanogr. Mar. Biol.* 46, 203–250.
51. Shaw, R.G., Geyer, C.J., Wagenius, S., Hangelbroek, H.H., and Etterson, H.H. (2008). Unifying life-history analyses for inference of fitness and population growth. *Am. Nat.* 172, E35–E47.
52. Kamel, S.J., Grosberg, R.K., and Marshall, D.J. (2010). Family conflicts in the sea. *Trends Ecol. Evol.* 25, 442–449.
53. Blows, M.W. (2007). A tale of two matrices: multivariate approaches in evolutionary biology. *J. Evol. Biol.* 20, 1–8.
54. Hilbish, T.J., Winn, E.P., and Rawson, P.D. (1993). Genetic variation and covariation during larval and juvenile growth in *Mercenaria mercenaria*. *Mar. Biol.* 115, 97–104.
55. Kraaijeveld, A.R., and Godfray, H.C.J. (1997). Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. *Nature* 389, 278–280.
56. Phillips, P.C. (1998). Genetic constraints at the metamorphic boundary: Morphological development in the wood frog, *Rana sylvatica*. *J. Evol. Biol.* 11, 453–463.
57. Levin, L.A., Zhu, J., and Creed, E. (1991). The genetic basis of life-history characters in a polychaete exhibiting planktotrophy and lecithotrophy. *Evolution* 45, 380–397.
58. Ernande, B., Clobert, J., McCombie, H., and Boudry, P. (2003). Genetic polymorphism and trade-offs in the early life-history strategy of the Pacific oyster, *Crassostrea gigas* (Thunberg, 1795): a quantitative genetic study. *J. Evol. Biol.* 16, 399–414.
59. Johnson, D.W., Christie, M.R., Moye, J., and Hixon, M.A. (2011). Genetic correlations between adults and larvae in a marine fish: potential effects of fishery selection on population replenishment. *Evol. Appl.*, in press.
60. Svane, I., and Young, C.M. (1989). The ecology and behaviour of ascidian larvae. *Oceanogr. Mar. Annu. Rev.* 27, 45–90.
61. McEdward, L.R., and Herrera, J.C. (1999). Body form and skeletal morphometrics during larval development of the sea urchin *Lytechinus variegatus* Lamarck. *J. Exp. Mar. Biol. Ecol.* 232, 151–176.
62. Jacobs, M.W., Degnan, S.M., Woods, R., Williams, E., Roper, K.E., Green, K., and Degnan, B.M. (2006). The effect of larval age on morphology and gene expression during ascidian metamorphosis. *Integr. Comp. Biol.* 46, 760–776.
63. Azumi, K., Sabau, S.V., Fujie, M., Usami, T., Koyanagi, R., Kawashima, T., Fujiwara, S., Ogasawara, M., Satake, M., Nonaka, M., et al. (2007). Gene expression profile during the life cycle of the urochordate *Ciona intestinalis*. *Dev. Biol.* 308, 572–582.
64. Jackson, D.J., Worheide, G., and Degnan, B.M. (2007). Dynamic expression of ancient and novel molluscan shell genes during ecological transitions. *BMC Evol. Biol.* 7, 340–348.
65. Havenhand, J.N. (1995). Evolutionary ecology of larval types. In *Ecology of Marine Invertebrate Larvae*, L.R. McEdward, ed. (Boca Raton: CRC), pp. 79–122.
66. Arnold, S.J. (1992). Constraints on phenotypic evolution. *Am. Nat.* 140, S85–S107.
67. Snoke Smith, M.S., Zigler, K.S., and Raff, R.A. (2007). Evolution of direct-developing larvae: selection vs loss. *Bioessays* 29, 566–571.
68. Phillips, P.C., and Arnold, S.J. (1989). Visualizing multivariate selection. *Evolution* 43, 1209–1222.
69. Blows, M.W., and Brooks, R. (2003). Measuring nonlinear selection. *Am. Nat.* 162, 815–820.
70. Rausher, M.D. (1992). The measurement of selection on quantitative traits – biases due to environmental covariances between traits and fitness. *Evolution* 46, 616–626.
71. Podolsky, R.D. (2001). Evolution of egg target size: an analysis of selection on correlated characters. *Evolution* 55, 2470–2478.
72. Johnson, D.W., Christie, M.R., and Moye, J. (2010). Quantifying evolutionary potential of marine fish larvae: heritability, selection, and evolutionary constraints. *Evolution* 64, 2614–2628.
73. Lynch, M., and Walsh, B. (1998). *Genetics and Analysis of Quantitative Traits* (Sunderland, Mass: Sinauer Assoc. Inc.).
74. Galletly, B.C., Blows, M.W., and Marshall, D.J. (2007). Genetic mechanisms of pollution resistance in a marine invertebrate. *Ecol. Appl.* 17, 2290–2297.
75. Miles, C.M., and Wayne, M.L. (2009). Life history trade-offs and response to selection on egg size in the polychaete worm *Hydroides elegans*. *Genetica* 135, 289–298.
76. Hoekstra, H.E., and Coyne, J.A. (2007). The locus of evolution: evo devo and the genetics of adaptation. *Evolution* 61, 995–1016.
77. Fellous, S., and Lazarro, B.P. (2011). Potential for evolutionary coupling and decoupling of larval and adult immune gene expression. *Mol. Ecol.* 20, 1558–1567.
78. Allen, R.M., and Marshall, D.J. (2010). The larval legacy: Cascading effects of recruit phenotype on ecological interactions. *Oikos* 119, 1977–1983.
79. Selkoe, K.A., Gaines, S.D., Caselle, S.D., and Warner, R.R. (2006). Current shifts and kin aggregation explain genetic patchiness in fish recruits. *Ecology* 87, 3082–3094.
80. Flowers, J.M., Schroeter, S.C., and Burton, R.S. (2002). The recruitment sweepstakes has many winners: Genetic evidence from the sea urchin *Strongylocentrotus purpuratus*. *Evolution* 56, 1445–1453.
81. Marshall, D.J. (2006). Reliably estimating the effect of toxicants on fertilization success in marine broadcast spawners. *Mar. Pollut. Bull.* 52, 734–738.
82. Byrne, M. (2011). Impact of ocean warming and ocean acidification on marine invertebrate life history stages: Vulnerabilities and potential for persistence in a changing ocean. *Oceanogr. Mar. Biol. Annu. Rev.* 49, 1–42.
83. Marshall, D.J. (2008). Transgenerational plasticity in the sea: a context-dependent maternal effect across life-history stages. *Ecology* 89, 418–427.
84. Marshall, D.J., Heppell, S., Munch, S.B., and Warner, R.R. (2010). The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? *Ecology* 91, 2862–2873.
85. Pandolfi, J.M., Connolly, S.R., Marshall, D.J., and Cohen, A.L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science* 333, 418–422.