CHAPTER 4

Evolutionary Transitions in Mode of Development

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4.1 Introduction

Since the field of larval biology was first framed by Thorson (1946; 1950), much attention has focused on the strategies that marine invertebrates employ to transform an egg into a juvenile. Because these strategies can generally be placed into one of two more-or-less discrete categories (planktotrophic and lecithotrophic; see Table 4.1), a main line of inquiry has been to understand the ecological and evolutionary mechanisms underlying transitions between these strategies. A large body of literature has focused on studies of the evolutionary origin, loss, and potential regain of feeding larvae. In this chapter, we argue that in the past, most of the focus has typically been on the long view; that is, evolution of complex larval traits is generally discussed in the context of phylogenetic patterns that have formed over long evolutionary timescales, and that are detectable when making comparisons within families, classes, or phyla. We increasingly use an analytical approach incorporating comparative phylogenetics to address these long-view questions. Such an approach is necessary for studies of the origin of larval types and broad macroevolutionary patterns, but will not be as effective for understanding the selective forces causing evolutionary transitions in larval feeding modes or the evolutionary processes that facilitate or limit change. Here we discuss what has been learned from taking a comparative phylogenetic approach and the limitations of this approach. We propose that approaches based on a closer view—analyses based on genetic, morphological, and functional variation as well as selective forces that act on that variation among individuals, populations, or closely related congeners—are more appropriate to answer questions about mechanisms underlying the loss and regain of major complex characters such as feeding larvae.

Many groups of marine invertebrates include both species with planktotrophic larvae and species that lack a feeding larval stage, and a few groups also include unusual intermediates like facultative feeding larvae and polymorphic development (Allen and Pernet, 2007; Collin, 2012; Table 4.1). Nonplanktotrophic development has been variously subdivided in the literature, depending on whether larvae are pelagic or spend part or all of development in capsules, gel masses, or brooded; however, a commonly listed dichotomy is between planktotrophic and lecithotrophic (yolk-feeding) development, where lecithotrophy encompasses all nonplanktotrophic modes as well as nonfeeding planktonic larvae. Planktonic larvae are free-living animals with complex morphologies that are generally characteristic of a phylum, class, or family. Feeding larvae may live for days, weeks, months, or even years in the water column, whereas pelagic lecithotrophic larvae generally spend hours to days in the plankton (Olson, 1985; Strathmann and Strathmann, 2007; Neilson, this volume; Marshall et al., this volume). While the evolutionary loss of feeding is often the main focus of comparative studies (Strathmann, 1978; 1985; Wray, 1995; 1996; Rouse, 2000; Collin, 2004), the evolutionary loss of planktotrophic larvae entails not just the loss of feeding per se, but also loss or modification of other characteristics that are associated with planktotrophy such as

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Table 4.1 Summary of Terms as Used in This Contribution.

Term	Explanation
Planktotrophic development	Including a larval stage that swims and feeds on plankton
Lecithotrophic development = nonfeeding development	Development without feeding on plankton
Lecithotrophic larva	A free-living larva that does not feed on plankton
Protected development	Development that is maternally protected or encapsulated and does not include a planktonic larval stage
Embryo	Any developmental stage before hatching

swimming structures, anti-predatory defenses, maternal protection, maternal investment, and many others (Strathmann, 1978; 1985), as well as likely modification of the genetic architecture underlying these traits (see Israel et al., 2016).

4.2 The Analytical Approach

Historical recognition of the gross morphological similarity between feeding larvae in each phylum or class, along with reduction in morphological complexity in those species that lack a feeding larval stage, has led to two main inferences from the long view: (1) the evolutionary transition from species with feeding to species with nonfeeding larval stages has happened multiple times in diverse lineages (Strathmann, 1978; 1985; Hart, 1996; Smith et al., 2007; Krug et al., 2015), and (2) the evolutionary reversal of this transition, or the regain of feeding larvae, is either very rare or impossible. The asymmetry in (2) has been attributed to Dollo's Law, which posits that complex characters that are not used are quickly lost and cannot be regained (Hart, 2000; Smith et al., 2007; Collin and Miglietta, 2008).

It is indeed difficult to imagine how the profound losses of characteristic larval structures in the most derived types of lecithotrophic development could be reversed to give rise again to the typical planktotrophic larval form for the group; in many taxa, nonfeeding larvae or embryos with nonfeeding development entirely lack the obvious structures used for feeding by planktotrophic larvae of related species. Examples of this include the loss of the long ciliated arms that are key to particle capture in the pluteus larva of planktotrophic echinoids and ophiuroids (Emlet, 1994; Hart, 2000; Selvakumaraswamy and Byrne, 2000; McEdward and Miner, 2001), loss of the shell and feeding apparatus of the bryozoan cyphonautes larva (Nielsen and Worsaae, 2010), and loss of the pilidium body form and ciliated lateral lobes necessary for particle capture in some lecithotrophic nemerteans (Maslakova and von Dassow, 2012; Martín-Durán et al., 2015; Maslakova and Hiebert, 2015). Many lecithotrophic larvae also lack a complete digestive system or functional gut, and in taxa that lack a free-living larval stage, the ability to swim has also frequently been lost (Moran, 1999; Chaparro et al., 2002; Hofstee and Pernet, 2011). Along with such dramatic morphological changes, other obvious but equally essential feeding characters are likely to be lost in many lecithotrophic taxa, including sensory, behavioral, or physiological pathways that facilitate feeding, though these types of characters have received less attention.

Although it is indisputably difficult to imagine evolutionary pathways that could lead to the reversal of the loss of complex suites of larval feeding structures, this failure of our imaginations is likely a function of taking the long rather than the closer view of the evolutionary dynamics of mode of development. Here we discuss results of recent phylogenetic studies that test the three major predictions derived from the traditional long view that feeding larvae are lost but not regained. We describe the strengths and weaknesses of this approach for testing the general theory of irreversibility of the loss of larval feeding and other transitions in mode of development.

Prediction #1: Species lacking feeding larvae should be nested within clades of species with feeding larvae; species with nonfeeding development should not be reconstructed as the ancestors of species with feeding development.

Most types of feeding larvae (e.g., echinopluteus, veliger, pilidium, actinotroch) are widespread in their phylum or class and appear to have evolved only once, and long ago (Strathmann, 1978; 1993). However, phylogenetically widespread does not necessarily equate to ancestral, and formal phylogenetic analyses followed by ancestral character-state reconstructions are necessary to determine whether lecithotrophic species are nested within clades of species with feeding larvae. Analytical methods of ancestral trait reconstruction must then be applied to assess the direction of character-state change.

Such approaches have been used in efforts to unravel the evolution of mode of development within a number of gastropod taxa; surprisingly, however, these analyses have been carried out in only a handful of other taxonomic groups (Table 4.2). Overall, these analyses show that ancestral states can be reconstructed with high confidence if evolutionary transitions are infrequent. For example, in a molecular phylogeny of temnopleurid sea urchins, the ancestral mode of development was reconstructed as planktotrophic with complete certainty (Jeffery et al., 2003). The results of this analysis were

Table 4.2 A Summary of Phylogenetic Studies Used to Document Evolution of Mode of Development.

Group	Number of species included / included with developmental data	Phylogenetic coverage (total species in group)	Conclusions of comparative analysis	Reference
Gastropods				
Conus s.l.	70/60	8% (~750)	Planktotrophy lost often and recently.	Palumbi and Duda 1999
Calyptraeids	72/72	51% (~140)	Change too common to reconstruct patterns with confidence.	Collin 2004
Crepipatella	6/5	62% (8)	Planktotrophy regained once.	Collin et al. 2007
Sacoglossans	202/113	39% (~290)	Planktotrophy lost; often not regained.	Krug et al. 2015
Muricids	45/45	3% (~1600)	Planktotrophy evolved three times.	Pappalardo et al. 2014
Nucella	9/8	80% (10)	Transitions between lecithotrophy with large eggs and with nurse eggs are common.	Marko et al. 2014
Phestilla	6/4	100% (4)	No formal analysis; plantktotrophy regained twice.	Faucci et al. 2007
Bivalves				
Lasaea	27/27#	100% (23)	Three independent losses of planktotrophy; no regains.	Li and Ó Foighil 2016
Ostreidae	21/21	38% (~55)	Maternal care evolved once and is ancestral for the only lecithotrophic species.	Ó Foighil and Taylor 2000
Echinoderms				
Asterinids	28/150	19% (~150)	Results vary with model parameters.	Keever and Hart 2008
Macrophiothrix	15/9	20% (45)	No formal analysis; change is frequent.	Hart and Podolsky 2005
Temnopleurids	24/24	39% (61)	Planktotrophy is lost once; change is rare.	Jeffery et al. 2003
Bryozoans				
Gymnolaemate bryozoans	48/43	<1% (>5000)	Ancestral state is ambiguous with parsimony reconstruction.	Waeschenbach et al. 2012
Ascidians				
Styelidae & Molgulidae	45/45	10% (~400)	Swimming has been lost multiple times, but cannot be regained.	Maliska et al. 2013

*Phylogenetic coverage is rough estimate, calculated as the number of species with developmental data in the phylogeny divided by the total number of species in the group (obtained from the cited reference or from WoRMS).

#Number of asexual lineages. Since lineages may not coincide with named species, this could result in an upward bias in taxonomic coverage.

clear because there was only a single loss of feeding in the phylogeny, and all descendants of that node were also nonfeeding (Jeffery et al., 2003). Ancestral states can also be reconstructed with high confidence when one state substantially outnumbers the other, as occurs in plakobranchacean sea slugs (Krug et al., 2015). In this clade, 21 of 62 taxa for which developmental information is available are lecithotrophic. An evolutionary quantitative genetics model reconstructed ancestral character states as planktotrophic at many internal nodes with posterior probabilities greater than 95% (Krug et al., 2015). In contrast, ancestral states in the sister group, Oxynoacea, which includes seven lecithotrophic species and nine planktotrophic species, could not be reconstructed with any certainty; both states were equally likely at many nodes (Krug et al., 2015). Analyses of other groups in which mode of development is highly variable have also generally failed to assign ancestral character states with confidence, including calyptraeid gastropods (Collin, 2004), muricid gastropods (Pappalardo et al., 2014; in their Figure 4.2), bryozoans (Waeschenbach et al., 2012), and asterinid sea stars (Keever and Hart, 2008). Recent analysis of continuous characters (e.g., egg size and number) suggests that use of continuous characters and the inclusion of other life history traits that might promote or constrain evolutionary transitions in the focal character may be powerful aids to reaching a fuller understanding of the subtleties of the evolution of development (Marko et al., 2014; Krug et al., 2015).

Prediction #2: Reconstructed rates of transitions between modes of development should be highly asymmetrical.

If (as seems likely) evolutionary transitions from planktotrophy to lecithotrophy are more probable than reversals, or if reversals are impossible, specific patterns should be recovered by analyses of character-state evolution. Support for irreversibility could be found in two aspects of a given analysis. First, likelihood and Bayesian models of character evolution provide a platform to determine if the data are best fit by a single-rate or a two-rate model. A single-rate model is favored when the data do not support different rates of transitions and their reversals. When the data favor unequal rates of transitions and reversals, a two-rate model is favored. Irreversibility would be supported if the estimated rate of transitions far exceeds the rate or reversals or if the rate of reversals is estimated as zero. Second, given a particular distribution of traits on a phylogeny, likelihood ratio tests can be used to compare the fit of different models of evolution between an irreversible model and an unconstrained model that allows both transitions and reversals. Phylogenetic analyses that have taken these approaches have generated a variety of estimates of rates of transitions and reversals and may also produce results that seem contradictory. In temnopleurid sea urchins, the group in which a clade of lecithotrophs is nested within a clade of pure planktotrophs, the one-rate model fits significantly better than a two-rate model, showing that the null hypothesis that losses and regains are equally likely cannot be rejected (Jeffery et al., 2003). In contrast, the irreversible model of character change fit the data significantly better than the unconstrained model (as only one transition and no reversals were evident), providing support for the idea that reversals do not occur (Jeffery et al., 2003). These different results may be due to the small number of changes, limiting the power of the test to reject the single-rate model. However, in a larger phylogeny of calyptraeid gastropods, the single-rate model was also the best fit for both gains and losses of planktotrophy and gains and losses of the ability to swim (Collin, 2004).

Mode of development may show patterns of phylogenetic correlation with other features like extracellular yolk (ECY) (Krug et al., 2015) or soft vs. hard substrate (Pappalardo et al., 2014). For example, in muricid gastropods the estimated rates of change between pelagic and benthic development were virtually zero in both directions for species living on hard bottoms, but estimated transitions from benthic to pelagic development were significantly greater than transition to benthic development in species living on soft bottoms (Pappalardo et al., 2014). Unfortunately, scant taxonomic sampling makes these results difficult to interpret. A study of sacoglossan sea slugs with substantially more thorough taxonomic sampling showed that models allowing covariance of lecithotrophy and ECY were highly preferred over those with independent evolution of the two traits: in the presence of ECY, lecithotrophy was twice as likely to evolve as it was in lineages lacking ECY (Krug et al., 2015). Likewise, in *Nucella* whelks, egg size and relative number of nurse eggs are significantly evolutionarily correlated (Marko et al., 2014). Nurse eggs are estimated to have been lost twice and significantly reduced in two other lineages; however, no estimates of the confidence in these reconstructions are reported (Marko et al., 2014).

Surprisingly, several phylogenies provide some support for a reversal: the evolution of planktotrophy from lecithotrophic ancestors. In two genera of calyptraeid gastropods there is clear evidence that planktotrophic species are nested deeply within clades of lecithotrophic species, and a likelihood reconstruction of the character states at specific nodes supports the re-evolution of feeding larvae in one genus (Collin et al., 2007), while a formal analysis has not been conducted on the other genus (Collin, 2005). A similar result was obtained by Faucci et al. (2007) who observed that two species of planktotrophic *Phestilla* were nested within a clade of lecithotrophic taxa, although the small number of species in this genus suggests that a formal analysis may not resolve the ancestral states with any confidence. Notably, in both of these analyses, lecithotrophic species were more numerous than planktotrophs. In the sacoglossan sea slugs and *Conus* (Palumbi and Duda, 1999), where planktotrophs predominate, no patterns of reversals are recovered. It is not clear if this represents an analytical artifact or a difference between the mechanisms driving life history evolution in these taxa.

Prediction #3: Species with lecithotrophic development should lose the structures used for feeding, but retain vestigial features that indicate descent from planktotrophic ancestors.

Overall, the literature shows strong support for this prediction. Numerous studies of comparative embryology and larval biology show that characteristic features of feeding larvae are reduced or (incompletely) lost in species with lecithotrophic development. Features used for swimming are also lost in species with benthic development. However, groups vary considerably in the degree to which larval features are lost, and this may in turn influence the probability of regaining feeding in lecithotrophic lineages (Collin and Miglietta, 2008).

The most well-studied examples of feeding-structure loss come from sea urchins. The characteristic larval form of sea urchins, the echinopluteus, is conserved across all echinoid families, suggesting this is a plesiomorphic character for the group. In lecithotrophic species, larvae often lack arms or guts (Emlet, 1994; McEdward and Miner, 2001). However, on close examination, vestiges of feeding structures such as arm spicules are present even in the most derived lecithotrophic echinoid larvae (Emlet, 1995). This is also the case in other classes of echinoderms such as asteroids and ophiuroids, where some lecithotrophic larvae have retained many features of planktotrophs but others are so altered as to be almost unrecognizable (McEdward and Miner, 2001; Selvakumaraswamy and Byrne, 2004; Byrne, 2006). In a larger but less thoroughly studied group, the gastropods, the characteristic feeding structure is the velum. The velum is generally present in lecithotrophic larvae, probably because it retains a swimming function, although it tends to be smaller and less elaborate than in planktotrophs (Moran, 1999). The velum is also retained in many species with encapsulated lecithotrophic development (Moran, 1999; Chaparro et al., 2002), but in other species, all outwardly visible vestiges of the velum are lost (e.g., Collin, 2000; Figure 4.1). Similarly, in lecithotrophic larvae of bryozoans and nemerteans, the characteristic feeding structures of the planktotrophic larva are absent, and in many of these lecithotrophic taxa, the larva bears little resemblance to the planktotrophic form (Zimmer and Woollacott, 1977; Maslakova and Hiebert, 2015).

4.3 Limitations of the Long View

There are a number of challenges to taking the broad approach to studying evolutionary transitions in mode of development. For transitions that likely happened many tens or hundreds of million years ago, such as the presumed loss of feeding larvae by an entire class of echinoderms (Crinoidea; McEdward and Miner, 2001), these challenges are perhaps insurmountable due to the difficulty in reconstructing ancient events. However, for more recent (but still long-view) transitions, impediments to inferring ancestral states fall into two main groups: (1) the fact that phylogenies of many (most) marine invertebrate taxa

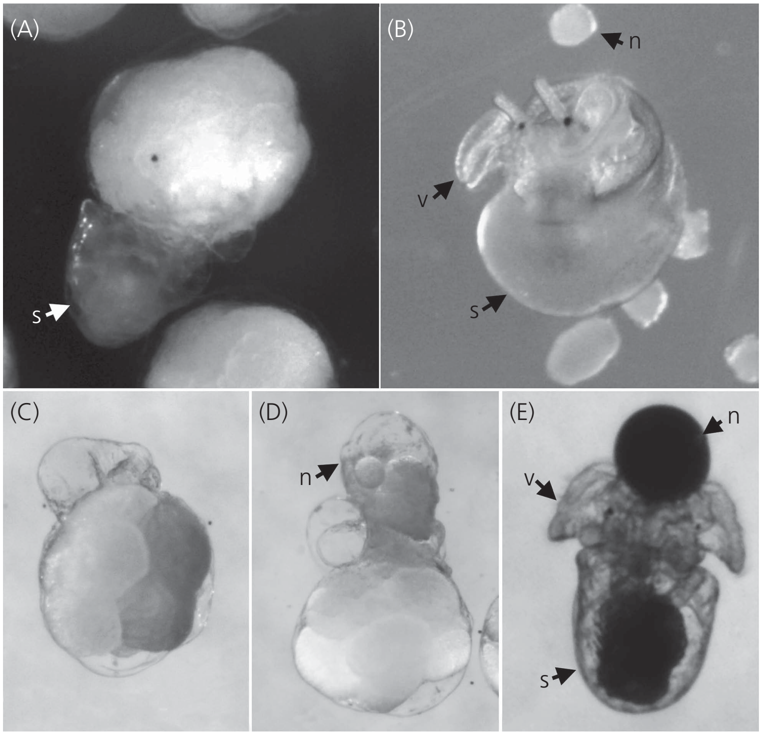

Figure 4.1 Lecithotrophic modifications of embryos in three adelphophagic calyptraeid species. A. Mid-stage embryo of *Crepidula coquimbensis* lacks a velum entirely. The velum would be clearly visible in the same stage of an embryo of species with planktotrophic development. B. Late-stage embryo of *Bostrycapulus odites*, which retains a small but distinct velum. C. Early stage of *C. coquimbensis* at which the embryo has already begun to ingest siblings. D. Early-stage *C. coquimbensis* embryo ingesting a sibling nurse embryo. E. A mid-stage embryo of *Crepipatella dilatata* using the velum to position a nurse egg for ingestion. v = velum; s = shell, n = nurse egg/embryo.

are woefully incomplete, and (2) shortcomings inherent to most methods of character-state reconstruction.

Comparative data from a growing number of genera or families indicate that in at least some cases, transitions in mode of development occur often and rapidly. This means that the results of comparative phylogenetic approaches could be significantly impacted by taxa that are missing from the phylogeny, or for which mode of development is not known. Only a small number of published analyses include 50% or more of the currently recognized species in the genus or family under study (Table 4.2). Understandably, studies with dense taxonomic coverage of extant species are those focused on small taxa (e.g., a genus with only a handful of species; Marko et al., 2014; Faucci et al., 2007), and this may limit both the power of the analysis and the opportunity to capture rare evolutionary events. Even if all living species in a taxon were included in a phylogeny and the developmental mode was known for all the species, comparative phylogenetic studies may still be compromised by incomplete taxon sampling due to loss of species through extinction. In some cases (e.g., bivalves, shelled gastropods, some echinoids, brachiopods, and bryozoans) it is possible to determine developmental mode from fossil morphology, but this is generally not the case. It is also difficult to include fossil taxa with any confidence in phylogenies of extant taxa generated from DNA sequence data, and it is not generally possible to generate well-estimated branch lengths with fossil data, as is required for most methods of ancestral state reconstruction. Overall, because sampling needs to be dense relative to the events of interest (transitions in mode of development), the comparative phylogenetic approach may be useful in groups where evolution in mode of development is slow and changes occur infrequently. To be effective in taxa where changes in mode of development are rampant, extremely dense taxon sampling of recent clades where extinction is thought to be minimal is likely the best approach.

Methods for reconstructing character-state evolution have come a long way in the last 20 years. In particular, current methods have made substantial progress toward addressing the circularity inherent in early attempts at using parsimony to describe asymmetry in frequencies of transitions and reversals (Strathmann and Eernisse, 1994; Cunningham et al., 1998; Cunningham, 1999; Collin and Miglietta, 2008; Keever and Hart, 2008). However, modern methods and the ways they are used to examine character evolution still make assumptions about the pattern of character-state evolution and are subject to bias from phylogenetic uncertainty (Duchêne and Lanfear, 2015). A clear example of the importance of model selection: Keever and Hart (2008) used asterinid sea star phylogenies to illustrate the importance of differentiating between (1) the use of phylogenetic comparative analyses to determine which model of character evolution is supported by the data and (2) their use to reconstruct ancestral states at specific nodes. They clearly demonstrated that using a model based on our heuristic understanding of larval biology (incorporating the idea that characteristic larval morphologies may be difficult for lecithotrophs to regain) produces different results from application of a model with unconstrained rates. Reconstructions of character evolution in sacoglossans also depended on the model selected; the unconstrained model estimated the rate for loss of planktotrophy as lower than the rate of reversals, a result considered to be biologically unreasonable by Krug et al. (2015). In addition, both rates were very high. A model that prohibited reversals estimated the rates of losses as about 1/10 of those estimated by the unconstrained model, clearly showing the impact of model choice on both the estimated rates and directions of change (Figure 5 in Krug et al., 2015).

Researchers agree that accurate reconstruction of ancestral developmental mode requires a model of evolution that is corroborated with independent traits, but anything more than the simplest models have yet to be developed (Collin, 2007; Keever and Hart, 2008; Krug et al., 2015; see following). Newly developed evolutionary quantitative genetic models may be more appropriate than discrete-state models for traits like mode of development because the longer a lineage drifts away from the character-state transition, the less likely reversals become (Revell, 2014; Krug et al., 2015). This matches our understanding that the likelihood of reversals decreases following the loss of feeding larval development, although it remains to be seen how accurately this approach models life history evolution.

Unfortunately, when more sophisticated models are developed, more sophisticated inputs are often necessary and more sophisticated problems arise. For example, a recent phylogenetic analysis of sacoglossans provided support for state-specific speciation and extinction rates. Such differences in rate could challenge estimates of character-state transitions. If speciation and extinction rates depend on the mode of development such that the derived state (lecithotrophy) has a lower diversification rate than the ancestral state, the phylogeny is likely to lack old lecithotrophic lineages. This pattern could bias estimated reversal rates upwards (Krug et al., 2015). Because differences in life history characters are thought to alter dispersal and gene flow and therefore impact speciation and extinction probabilities, state-specific extinction and speciation rates could potentially occur in many or most clades of marine invertebrates.

Summing up the long-view evidence, both the majority of the literature and common sense dictate that lecithotrophic taxa are generally derived from planktotrophic ancestors, and reversals are rare but perhaps not impossible. Supporting evidence comes largely from homologous feeding structures that are found across classes and from phylogenies where transitions are relatively rare and lecithotrophic development is uncommon. In these latter cases results are likely to be robust to the choice of model selection. However, comparative analyses of deeply intriguing taxa such as *Patiriella*, *Macrophiothrix*, and calyptraeids—where no one feeding mode dominates and transitions may be frequent—fail to provide support for the accepted view. Unfortunately, comparative methods are not yet likely to provide satisfying answers about evolutionary transitions in what are arguably the most interesting taxa: groups where life history characters evolve rapidly and transitions are common.

4.4 Future Directions and Unanswered Questions for Analytical Approaches

The development of more sophisticated methods for comparative analyses now allows some longstanding questions in larval biology to be addressed. First, it has been widely accepted that (1) species with lecithotrophic development have lower levels of dispersal and gene flow than do planktotrophic species (Collin, 2001; Selkoe and Toonen, 2011; Ellingson and Krug, 2015), and that (2) this results in higher rates of speciation and/or extinction in lecithotrophic species than in planktotrophic species (Hansen, 1980; Jablonski and Lutz, 1983; Marko and Moran, 2009). However, two recent comparative analyses testing for state-specific rates of diversification (speciation-extinction), have shown that diversification rates are lower in species with development resulting in lower dispersal. In sacoglossans, lecithotrophic slugs have lower diversification rates compared to planktotrophs (Krug et al., 2015). In fact, higher extinction rates lower the net diversity of lecithotrophs despite the fact that lecithotrophy originates frequently. Krug et al. (2015) suggest that this pattern could explain the long-term maintenance of planktotrophy in clades despite the fact that loss of planktotrophy is a frequent event. Species selection against a trait that reduces dispersal has also been demonstrated in ascidians, where speciation rate is higher and range size is larger in species with tailed tadpoles than in those whose development lacks a tailed swimming larva (Maliska et al., 2013). The apparent discordance between results from fossils, population genetics, and comparative phylogenetics needs to be investigated in more detail. It is possible that this discordance is due to specific features of the biology of sacoglossans (many are obligate specialist herbivores) or tunicates (many are fouling organisms subject to rafting). Clearly, a concerted effort must be made to generate large, densely sampled phylogenies, especially for taxa with extensive background data on population genetics and larval biology, so that similar tests on other taxa can be performed.

Second, in order for phylogenetic models to perform well, it is necessary to have well-characterized traits. It may be both appealing and ecologically relevant to dichotomously classify development as planktotrophic vs. lecithotrophic, pelagic vs. benthic, or brooded vs. broadcasted, but a potential downfall of using discrete classification is that it can become implicit in the phylogenetic method that the states are homologous. For example, gastropods that develop without a feeding larval stage from large eggs and those that develop from small eggs with embryos that consume each other would both be coded as "nonplanktotrophic." Therefore, use of continuous measures like egg size or nurse egg number (Marko et al., 2014; Krug, 2015), and more nuanced descriptions of development that separate modes of development into multiple discrete states (Collin, 2004; Keever and Hart, 2008) are likely to produce more robust results. In addition, simultaneous analyses of correlated characters or characters that may influence or constrain the trait of interest may significantly improve results (Ó Foighil and Taylor, 2000; Krug et al., 2015). Therefore, as much care should be put into coding characters—including the most appropriate traits as correlates—as is put into the analyses themselves.

Finally, questions about whether shifts in mode of development are associated with the process of speciation, and if shifts occur during gradual change in a species or divergence in isolated peripheral populations, are also understudied. Since closely related sister species often differ in mode of development in speciose clades, it is possible that changes in mode of development contribute to speciation. The largest study to explicitly address this question across a deep phylogeny found that models allowing divergence in mode of development at nodes as well as along branches did not perform any better than a model that allowed change only along branches (Krug et al., 2015), though a model where change occurred only at nodes was not tested. Further detailed study of populations of slugs in the process of diverging suggested that reduction or loss of dispersal associated with a shift toward aplanktic development could increase local recruitment and inbreeding, leading to the evolution of reproductive isolation (Ellingson and Krug, 2015). More detailed studies of this kind are necessary to assess this possibility. Detailed genome scans of closely related species are now possible for non-model taxa, and are likely to provide exciting new insights into what genes are under selection in diverging or recently diverged taxa, potentially clarifying links between shifts in developmental mode and speciation (Zakas and Rockman, 2015).

4.5 A Closer View

We argue that unlike the deep questions surrounding the origin of larval feeding modes in large clades such as echinoids, gastropods, bryozoans, etc., which have the potential to be answered by combining data from phylogenies, the fossil record, and morphological evidence from modern taxa, many questions about life history transitions are essentially shallow ones that hinge on microevolutionary processes. If we are really to understand the causes and processes involved in transitions between modes of development, it is important to use what we have learned from broad comparative analyses to look closely at divergence in action. Ideally, the broadly comparative analytical and the more detailed descriptive views can be reciprocally illuminating: phylogenetic analyses can help identify species or small sub-clades that are of particular interest, and detailed analyses at the population or species level can provide a close-up view of the underlying genetic, morphological, and functional variation, and selective forces that act on that variation. In the rest of this chapter we list some major unanswered questions that we feel would benefit from greater research emphasis on closer detailed descriptions and microevolutionary approaches.

Question #1: Does the order of transitional steps in the evolution of direct development differ among taxa, and what selective forces act along the way?

When using modern comparative phylogenetic methods to understand character-state evolution, two key factors are coding the characters and choosing a model of character-state transformation. At the most basic this includes the null model of losses and reversals being equally likely vs. the hypothesis that losses are irreversible. If there is a continuum of character states (e.g., egg size) along which planktotrophic species must move in order to eventually make the switch to lecithotrophy (e.g., brittle stars which may include an ophiopluteus which may or may not feed and/or a distinct vitellaria stage; McEdward and Miner, 2001; Selvakumaraswamy and Byrne, 2004), or if species find alternative solutions to the same problem (e.g., gastropods where lecithotrophic development can proceed from large eggs or from small eggs with adelphophagy), the way the characters are scored can significantly impact the conclusions of the study (e.g., Collin, 2004; Keever and Hart, 2008). Once the characters are coded, comparative methods can be used to determine the rates of character-state transformations that are best supported by the data (phylogeny and the character states of the operational taxonomic unit (OTUs)). However, this approach ignores any independent knowledge we have about the likelihood of the transitions, and when this information is included in a crude way, the results of the comparative analyses often differ (e.g., Krug et al., 2015).

Computational biologists are constantly working to refine the way independent data can be incorporated into such analyses, but larval and developmental biologists need to put effort into refining evidence and developing formal models of how evolutionary transitions among modes of development work. This includes articulating explicit models of how different developmental morphologies are related to each other, postulating the selective forces that are acting most strongly on different kinds of development, and developing hypotheses about the selective factors that could drive evolutionary change. At this point heuristic models have been developed for sea urchins (Smith et al., 2007) and sea stars (Keever and Hart, 2008). The overall paradigm based on these echinoderms roughly posits that changes occur in this order: (1) energy content of eggs increases; (2) development to metamorphosis accelerates; (3) the requirement/ability to feed is lost; (4) time to metamorphosis is shortened by additional reduction of larval structures (Smith et al., 2007). In order to adapt this heuristic model of transitions between modes of development to other taxa, features relevant to those taxa need to be considered. For many groups these include encapsulation or maternal protection and extraembryonic nutrition (extracellular yolk; nurse eggs; matrotrophy). Some differences in the factors that are most likely under selection during different stages and kinds of development are presented in Figure 4.2. It is important to emphasize that few detailed datasets have been developed to describe these steps and that heuristic schemes describing evolutionary trajectories are generally based on logical interpretations of known larval morphologies (McEdward and Janies, 1993; McEdward and Miner,

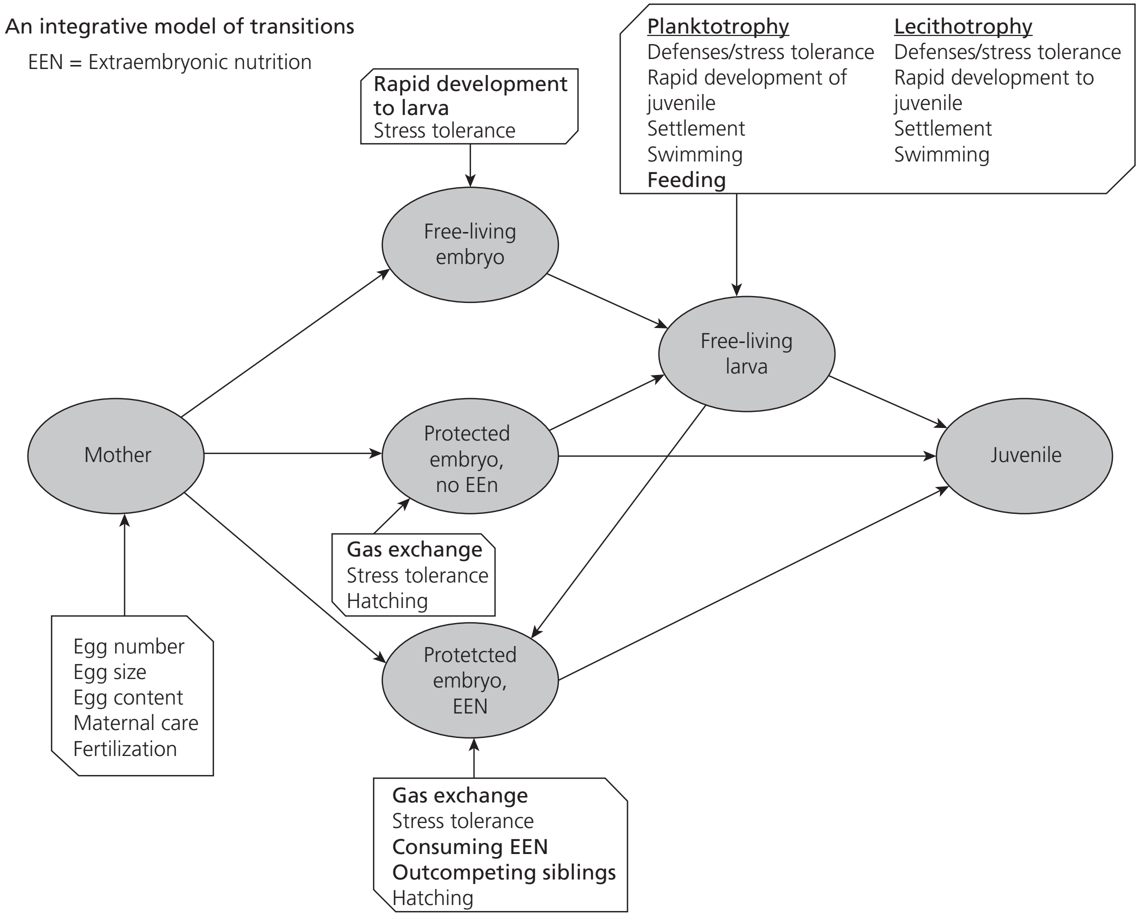

Figure 4.2 Alternative pathways of larval development from egg to juvenile and the major features under selection at each stage. Defining or unique selective forces for each stage are indicated in bold.

2001; Smith et al., 2007). Larry McEdward was a major proponent of this approach (McEdward and Janies, 1993; McEdward and Miner, 2001) and his heuristic models still form an important framework for explicit hypothesis testing. Similar detailed efforts are needed to provide clear models for non-echinoderm taxa that could help to inform more sophisticated comparative analyses.

Question #2: What features other than gross larval morphology change during transitions in mode of development?

The major focus of marine invertebrate biologists working on the evolutionary transitions between modes of development has been the gross morphology of the embryos and larvae, and in particular the structures used for feeding and swimming. However, changes in numerous other features may occur either via genetic drift or through active selection for alternate function. Understanding these may help further refine our view of how selection acts on small details of development and ultimately produces transitions between modes of development. While egg size has long been a focus of life history studies, one related character that has received considerable attention in recent years is the biochemical composition of the egg.

The major constituents of eggs are protein, lipid, and carbohydrate, and the proportion and type of these constituents is correlated with developmental mode in what is generally interpreted as an adaptive way. As one broad example, the eggs of lecithotrophic species generally contain proportionally more lipid, which is thought to provide energy for the metamorph as well as the nonfeeding larva (Emlet and Hoegh-Guldberg, 1997; Moran and Manahan, 2003; Prowse et al., 2008; Moran et al., 2013; Falkner et al., 2015) and has also been implicated in buoyancy (Arai et al., 1993). Feeding larvae, in contrast, contain proportionally more protein and build lipid reserves through feeding (Jaeckle, 1995; Moran and Manahan, 2004; Sewell, 2005; Moran et al., 2013). Lipid profiles also differ by taxon and mode of development; for example, in asterinid sea stars, triglycerides are relatively more abundant in eggs of most lecithotrophic species than in planktotrophic species (Prowse et al., 2008), while some lecithotrophic ophiuroids supply eggs with wax esters, a lipid class not found in planktotrophs (Falkner et al., 2015). As another example, thyroid hormones are required for metamorphosis in many echinoderms (Heyland et al., 2004). For planktotrophic species, these hormones are acquired through feeding; in lecithotrophs, exogenous acquisition has been replaced by endogenous production (Heyland et al., 2004; Armstrong and Lessios, 2015).

Other changes we might expect with the switch to lecithotrophy are the loss of larval sensory structures and threat responses in species with protected development. Species lacking free-living larval stages may also show loss or reduction of the pathways associated with triggers for settlement and metamorphosis (see Section 3 of this volume), as well as changes in the genetic architecture, maternal provisioning of mRNA, cell fates, and other components of development. For example, in *Heliocidaris* the animal-vegetal axis is maternally specified in the planktotrophic species, while in the lecithotrophic species the dorso-ventral axis is also maternally specified (Henry et al., 1990). Clearly, the loss of feeding larvae is accompanied not just by morphological changes to larvae, but also by more subtle physiological changes, as well as alterations to gene expression, maternal oogenetic pathways, and maternal reproductive morphology. The evolutionary lability of these less visible features has rarely been explored, but they may play a major role in determining the probability and direction of transitions in life history characters.

Question #3: If planktotrophy were to re-evolve, how would it happen and how could we recognize it?

Thought exercises exploring possible routes to the re-evolution of feeding larvae have been performed over deep phylogenies (Strathmann, 1978). Two primary routes have been considered: larvae of a non-planktotrophic species could regain function of vestigial feeding structures, or larvae could regain feeding through co-option of juvenile or adult feeding structures. For many taxa, the striking reduction or loss of larval feeding structures suggests that co-option of juvenile features may be the only option available for re-evolving feeding larvae. This may have occurred in the ancestors of modern clades of inarticulate brachiopods, cerianthid cnidarians, and cephalopods, all of which have feeding larvae which are strikingly similar to their juveniles. This option, however, is not equally open to all taxa; for example, in echinoderms the juvenile feeding structures appear to be poorly suited for planktonic feeding (Strathmann, 1978). It may be noteworthy that no cases of the recent regain of feeding via "larvalization" of the juvenile has been reported in individual species or genera; however, one related example has been described in *Pteraster tessulatus*, in which nonfeeding larvalization has occurred through the recent evolution of a swimming juvenile (McEdward and Janies, 1993). Closer examination of these rare cases could provide important insight into the processes involved in transitions of early life history stages between the benthos and the plankton.

Re-evolution of planktotrophy may also happen through regain of function of vestigial feeding structures (Strathmann, 1978). It is intuitively apparent that the probability of regaining function would be negatively correlated with the degree of loss; thus, a facultatively feeding larva that is functionally lecithotrophic but can still feed would much more easily return to the planktotrophic state than a species whose lecithotrophic larvae have lost feeding structures and a functional gut (Strathmann, 1978; 1985). Similarly, encapsulated embryos that retain the larval structures and their function may facilitate re-evolution of larval feeding (Collin, 2004; Collin and Miglietta, 2008). In this case, however, it would be very difficult to distinguish a species that had transitioned back to planktotrophy based on morphology alone (McEdward and Janies, 1997).

A number of lecithotrophic species do seem to retain the unused potential for larval feeding and swimming (Hookham and Page, 2016). For example, embryos of many calyptraeid gastropods retain the ability to capture and ingest particles (Chaparro et al., 2002; Collin, 2004; Collin, unpublished data). Likewise, a number of taxa have recently been demonstrated to possess facultatively feeding larvae (Allen and Pernet, 2007). What, then, is needed to identify species that may have reverted back to planktotrophy from such a state?

We know of no example from the marine invertebrate larval literature, but one example from deep-sea worms illuminates how phylogenetic and morphological analyses can be used in concert to identify reversals of past changes to complex life history traits. Working with the siboglinid genus *Osedax*, a group of saprotrophic worms in which males of most species show extreme dwarfism as parasites on females, Rouse et al. (2015) demonstrated an evolutionary reversion from dwarf parasitic males (ancestral in this clade) to free-living full-sized males. The evidence came from phylogenetic analyses, in which a species with free-living non-dwarf males was nested within a clade of species with parasitic dwarf males, and from retention of the dwarf-style testicular structure on the males of the species that re-evolved large body size. A search for similar relic markers for direct development or lecithotrophy could help identify potentially re-evolved larvae that could be the focus of further study. For example, neutral lipid classes that are not present in eggs of planktotrophic ophiuroids occur in eggs of lecithotrophic species (Falkner et al., 2015); if a planktotroph's eggs were found to contain these "lecithotrophic" lipids, this could provide independent evidence for a phylogenetically based hypothesis for reversal (Keever and Hart, 2008), or could indicate a taxon in the early stages of transition. Similarly, in gastropods, the retention of globose protoconch shapes, or protoconchs lacking characteristic planktotrophic sculptures, may be evidence of reversions to planktotrophy (Reid, 1989). Finally, it would be interesting to know if it is possible to detect transitions in mode of development in taxa with morphologically simple larvae. For example, while many cnidarian larvae are morphologically similar, they vary significantly in their duration in the plankton as well as their reliance on yolk reserves, autotrophy, parasitism, and larval feeding (Baird et al., 2009). Due to their simple forms, these larvae have been largely overlooked in discussions of evolutionary transitions in mode of development, but they may be a taxon ripe for study.

Question #4: How do mode of metamorphosis and maternal protection influence the evolution of mode of development?

Three different factors may influence the modification of lecithotrophic developers compared to their planktotrophic ancestors: (1) natural selection for better performance in larval functions (e.g., swimming, settlement site selection) results in convergence on ball-like morphology and specific arrangements of ciliary bands; (2) natural selection for faster development to the juvenile stage selects for earlier allocation to juvenile structures and reduction of specific larval features; and (3) genetic drift in the genes underlying unused structures and functions. For most species with large population sizes, selection would be expected to act more quickly than genetic drift. The relative importance of these factors has been discussed for echinoid models, but they may be quite different in other taxa.

Echinoids are the model on which much of our current understanding has been built, as planktotrophs have unprotected, maximally indirect development. In species with feeding larvae the juvenile grows in a small pocket inside the larva. At metamorphosis the juvenile emerges from the pocket and the vast majority of the larval body is discarded. This suggests that the larval and juvenile bodies are largely independent and should be free to evolve independently. Therefore, if the larva no longer needs to feed, the developing juvenile is probably not strongly impacted by a reduction in the larval arms or rearrangement of the ciliary bands, and the gross morphology of the larva could be altered drastically. In fact, selection may act on a number of facets of development to speed the loss of larval features once the transition is underway, including selection for better swimming performance (Emlet, 1991; 1994) and selection for faster development of the juvenile (Raff and Byrne, 2006; Smith et al., 2007). Other larvae with similar development of the juvenile within but largely distinct from the larval body include the pilidium larva of nemerteans and mitraria of oweniid polychaetes. In nemerteans, lecithotrophic pilidia tend to converge on ciliated balls similar to those predicted to perform well at swimming (Emlet, 1991; Maslakova and Hiebert, 2014). Likewise, in lecithotrophic larvae of bryozoans and hemichordates, two other groups in which metamorphosis of a planktotrophic larva involves a drastic change in body plan, the lecithotrophic larvae appear to be optimized for swimming.

In contrast, larvae of a number of other groups have a body plan very similar to that of the juvenile. These include most polychaetes, gastropods, and polyclad flatworms in which the larval body is almost entirely the same as the juvenile body, but with the addition of ciliated bands and projections used for feeding and swimming. In these groups lecithotrophic developers do not evolve into yolky ciliated balls, and they generally retain the body form that is shared between the larva and the juvenile. In these cases natural selection for rapid development of the juvenile would not be expected to modify the body plan other than to perhaps reduce the size or complexity of the specific larval structures. In addition, in many of these groups the embryos are encapsulated, and it appears unlikely that natural selection would act to modify them for swimming. However, in many cases aspects of the encapsulated environment may act to retain larval structures (Figure 4.1); for example, the velum of gastropod larvae has a feeding function in many species where nutrition is extraembryonic (e.g., adelphophagy) and species may be selected for better and faster consumption of nurse eggs, extraembryonic yolk, or albumen (reviewed in Moran, 1999). The velum (or ciliary bands in other taxa) may also serve encapsulated embryos by stirring capsule fluid and providing a large ciliated surface for enhancing gas exchange (Hunter and Vogel, 1986; Moran, 1999; Hofstee and Pernet, 2011). The intracapsular environment may in some cases have selected for dramatic modification to the veliger form; for example, inter-sibling competition for early nurse egg consumption in adelophophagic embryos of *Searlesia dira*, and *Buccinum undatum* results in embryos that are bags of yolky eggs and hardly resemble early development of other gastropods at all (Rivest, 1983; Smith and Thatje, 2013; Figure 4.2). In general, however, in groups where the larval body plan is the same as the juvenile body plan, the retention of ancestral larval feeding and swimming structures appears to be common. Whether this is due to recent evolutionary origins of lecithotrophic development or unidentified functions of these structures—or whether these features are simply not visible to natural selection and take a long time to be lost by the slow accumulation of mutations via genetic drift—is an outstanding question.

Underlying all of these close-view questions is the issue of how microevolutionary processes produce evolutionary change in mode of development. McEdward (2000) explained the importance of combining quantitative models that analyze the selective factors that drive evolutionary change with understanding of the genetic architecture underlying the mechanisms of development. This is as true today as it was nearly 20 years ago. While the field of evo-devo has made rapid progress in understanding the genetic mechanisms of development, little progress has been made in understanding how selection acts on natural variation to generate divergent life histories. In the last 20 years, research on evolutionary transitions in mode of development has been focused fruitfully on comparative phylogenetic approaches. We hope that the next 20 years will see an equally fruitful focus on microevolutionary models to understand the evolutionary mechanisms of transitions in mode of development (e.g., Garfield et al., 2013; Arendt, 2015; Zakas and Rockman, 2015).

4.6 Summary

1. Despite the call for more phylogenetic analyses with dense sampling to understand evolution of mode of development by McEdward and Miner (2001), few such analyses have been published in the intervening 15 years.
2. Comparative analyses show well-supported patterns when transitions are rare but are not always able to reconstruct evolutionary patterns of mode of development with confidence when evolutionary changes are rapid and common.

3. Improvements in phylogenetic comparative methods and wider sampling are likely to improve the utility of this approach, but significant weaknesses remain.
4. Overview of the published analyses shows that the "what makes sense" view of macroevolutionary patterns of the evolution of mode of development are not always supported. For example, contrary to what makes sense, planktotrophic species showed a higher diversification rate than lecithotrophs in sacoglossans (Krug et al., 2015).
5. Increased effort to examine closely the microevolutionary processes involved in transitions and the mechanisms like pleiotropy, plasticity, and balancing selection, which potentially play a role in the retention of reversal ability—another area of study advocated by McEdward (2000)—are likely to contribute significantly to our understanding.

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