



## SYMPOSIUM

### Nontraditional Life-History Choices: What Can “Intermediates” Tell Us about Evolutionary Transitions between Modes of Invertebrate Development?

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**Synopsis** Mode of development in marine invertebrates has been largely viewed as a dichotomy between small eggs that develop into free-living planktotrophic larvae and large eggs that bypass the larval stage and develop directly into juveniles. Modes of development that could be categorized as “intermediate” between these two extremes include facultative feeding larvae, short-lived planktotrophic larvae, dispersal dimorphisms, and poecilogony (in which nutritional mode varies within a species). These intermediates are rare. The few species-level phylogenies available that include them do not generally support the interpretation of intermediates as necessary, ephemeral transitional forms. Instead, they support the idea that intermediates are well adapted to their environments but that either these environments are short-lived relative to the frequency of speciation, or speciation events are associated with shifts in the mode of development. Each of the different intermediate forms could have evolved in response to variable environments. The phenotypically plastic intermediates could be a response to predictable environmental variation. Facultative feeding larvae and short-lived planktotrophic larvae could reflect conservative bet-hedging in response to unpredictable environmental variation, whereas poecilogony with mixed clutches could represent the alternative: diversifying bet-hedging. Since environmental variability is common, it remains an enigma why these intermediates are so rare. Discovery of more intermediates, and their careful description in terms of the level of variation expressed within, and among, clutches, and among females and populations, as well as determination of the genetic and environmental influences on this variation, will provide valuable test-cases for theories of the evolution of alternative phenotypes.

#### Introduction

Mode of development in marine invertebrates is traditionally classified into two main types based on a nutritional dichotomy (planktotrophy versus lecithotrophy) (Thorson 1950; Vance 1973a, b; Christiansen and Fenchel 1979). Species with planktotrophic development produce numerous small eggs. These develop into characteristic larvae that swim, feed, and grow in the plankton before settlement and metamorphosis. Planktotrophic development is considered to be the ancestral condition in most groups of invertebrates, and each class or phylum is characterized by a distinct larval form (Strathmann 1978a, b, 1985). Thorson (1950)

estimated that ~70% of marine invertebrate species have planktotrophic larvae. At the other extreme, species with lecithotrophic development produce fewer larger eggs that do not rely on exogenous food to develop (although they do sometimes feed on maternally provided nurse eggs or embryos). This kind of development is more variable and can include lecithotrophic swimming larvae or encapsulated, or brooded, development in which offspring hatch as crawling juveniles. In either case, lecithotrophic larvae or embryos often have lost many of the characteristic planktotrophic features of their close relatives.

The view of mode of development based on the dichotomy in larval nutrition combined with the

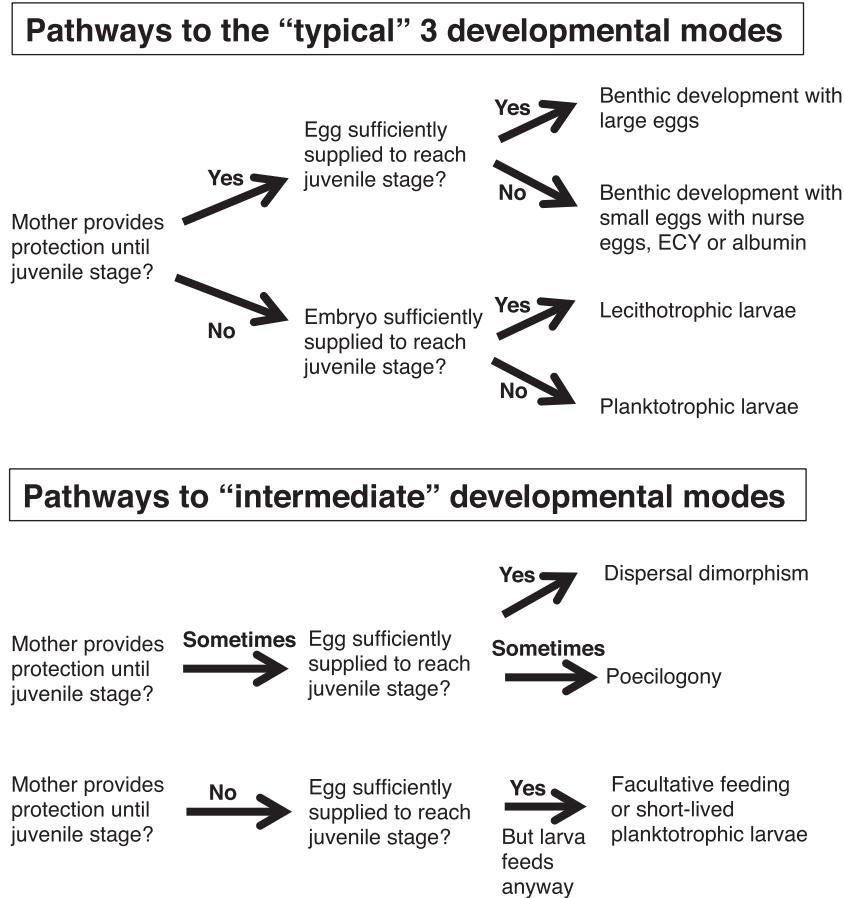
distinction between benthic versus pelagic development has been a useful way to categorize invertebrate development. Planktonic development can be either feeding or nonfeeding but benthic development is virtually never planktotrophic. The vast majority of eggs and embryos fall into one of these three categories. Additional dichotomies have been added to this scheme to help categorize the diversity in invertebrate development and to understand the place of intermediates (e.g., McEdward and Janies 1993; Poulin et al. 2001). This includes the distinctions between protected versus unprotected development (Poulin et al. 2001) and embryologically direct or embryologically indirect development (McEdward and Janies 1993). Indirect development includes development of a characteristic larval morphology or the morphological structures associated with feeding and swimming by the larvae. These structures are often lost or reduced in species with obligate lecithotrophic development (McEdward and Janies 1993). Many species that are traditionally considered to have ecologically direct development because they hatch as crawling juveniles actually develop indirectly through characteristic larval stages when encapsulated or brooded. Development that bypasses larval stages is sometimes called ametamorphic, a term common in the literature on opisthobranchs. The difference between direct and indirect is often not clear-cut, as many lecithotrophic embryos develop some reduced larval characters while completely bypassing others (Collin 2004).

Attempts to simplify the vast diversity of mode of development by applying all four dichotomies result in 32 separate categories. Poulin et al. (2001) who proposed 16 categories suggested that more than one category could be experienced during development, further increasing the possibilities. Because dichotomies are often artificially imposed on continuous variation in some features, these categories may not help clarify biologically relevant variation. Categorization of development based on the following two maternal dichotomies generates the three primary modes of development thought to include most species (Fig. 1) (Thorson 1950). (1) Does the mother provide protection until the juvenile stage is reached? and (2) Does the mother provide sufficient energy for the juvenile stage to be reached? Intermediate modes of development fit simply into this scheme (Fig. 1). Within these categories the embryos may fall anywhere on the continua from unprotected to well-protected, embryologically direct to indirect, poorly provisioned to well-provisioned, or poorly dispersing to highly dispersing.

## What are “intermediates”?

For the purposes of this article, intermediates in mode of development can be broadly categorized into three kinds that do not fall clearly into one of Thorson’s three primary modes of development (Fig. 1; Table 1):

- (1) Facultative feeding larvae and short-lived planktotrophs (*sensu* Thorson 1950) blur the line between lecithotrophy and planktotrophy. Facultative feeding larvae can metamorphose successfully without feeding, but can feed and derive measurable benefits from feeding (reviewed by Allen and Pernet 2007). Thorson (1950) described a distinct category of short-lived planktotrophic larvae that includes facultative feeding larvae, as those that have the morphology of typical planktotrophic larvae, but do not change in size or organization between hatching and settling. These larvae spend hours to a few days in the plankton during which time they may feed, but benefits of feeding have not been demonstrated;
- (2) Species with “dispersal polymorphisms” produce either larvae that swim when they hatch or that complete metamorphosis and lose the ability to swim prior to hatching (Krug 2009). This is often caused by a shift in the timing of hatching relative to metamorphosis, suggesting that the shift from swimming to nonswimming is not always as radical or irreversible as it first appears. In many cases, the larvae swim for a very short time. This dichotomy in swimming ability can occur within one egg mass, possibly in response to slightly different conditions experienced by each embryo within the mass. Differences in the stage at hatching have also been observed among populations (e.g., *Haminoea zealandiae* discussed by Clemens-Seely and Phillips [2011]). Finally, embryos within a single egg mass may have distinct behaviors. For example, in *Alderia willowi*, there appear to be two kinds of hatchlings, those that rapidly settle spontaneously and those that swim actively until encountering specific algal cues that trigger settlement (Krug 2001); and
- (3) In poecilogony more than one kind of development occurs in a single species. This has traditionally included species with plasticity or dimorphism in nutritional mode as well as species that show concomitant variation in nutritional and dispersal modes (Table 1). Type of offspring can vary in a single brood (e.g., *Boccardia proboscidea* [Gibson 1997] and *Boccardia polybranchia* [Duchène 1984]), can



**Fig. 1** Two maternal dichotomies generate the three main modes of development that encompass most variation in mode of development. The intermediate modes of development discussed here can be placed into the same scheme. Within each of these categories the embryos may fall anywhere on the continua from unprotected to well-protected, embryologically direct to indirect, poorly-provisioned to well-provisioned, or philopatric to highly dispersing.

change over the lifetime of a single female (e.g., *A. willowi* [Krug 1998, 2009] and some *Polydora cornuta* [Mackay and Gibson 1999]), and can vary among co-occurring females (e.g., most *P. cornuta* [MacKay and Gibson 1999], and *Streblospio benedicti* [Levin and Bridges 1994]) or among populations of the same species (e.g., *Pygospio elegans* [Morgan et al. 1999]).

These three kinds of intermediates may not at first glance appear to have much in common. However, they may all be viewed as possible evolutionary transitions between the three more common modes of development. As I will explain below, they also may represent alternative evolutionary responses to environmental uncertainty.

### How can intermediates fit into evolutionary transitional series?

Phylogenetic reconstruction of the evolution of mode of development offers the hope of increased

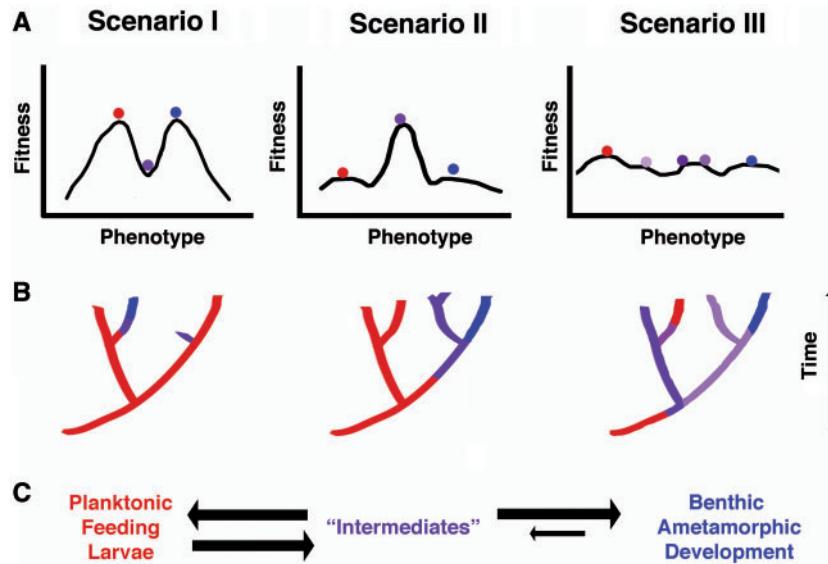
understanding of the role intermediate forms of development play in evolutionary transitions. The three main alternative hypotheses are as follows:

- (1) Intermediates might simply be a stage in the evolutionary transition between the two main evolutionarily and adaptively stable modes of development (Scenario I in Fig. 2) (Wray and Raff 1991; Hart 1996). Intermediates could then be considered as species caught in the act of crossing an adaptive valley. In this scenario, they should occur most frequently in groups that show high diversity in development. Because these transitions should be evolutionarily rapid, however, intermediates should rarely be observed and should appear as ephemeral, short twigs on phylogenies when they are observed (Hart 1996);
- (2) Alternatively, intermediates might be more responsive and finely tuned to the environment than are the two extremes (Scenario II in Fig. 2). In this case, they might experience the best of

**Table 1** Kinds of intermediates

	Nutritionally	Ecologically	Developmentally	Species
Facultative planktotrophy <sup>a</sup>	Nutritional Generalist: Each embryo can but does not have to feed.	Pelagic	Indirect	Echinoderms: <i>Clypeaster rosaceus</i> , <i>Brisaster latifrons</i> , <i>Macrophiothrix rhabdota</i> . Molluscs: <i>Adalaria proxima</i> , <i>Conus pennaceus</i> , <i>Phestilla sibogae</i> . Vertebrates: <i>Bufo periglenes</i>
Dispersal dimorphism <sup>b</sup>	Lecithotrophic	Within-brood plasticity: Each egg mass can include some swimming and some non-swimming offspring. The ability to swim at hatching seems to depend on physical conditions experienced and the degradation of the egg mass.	Indirect	Molluscs: <i>Haminoea japonica</i> , <i>Turbonilla</i> sp., <i>Berghia verrucicornis</i> , <i>Tenellia adspersa</i> (= <i>fuscata</i> of Haris 1980), <i>Elysia cornigera</i> .
	Lecithotrophic	Among-populations: Populations either produce swimming larvae or intracapsular metamorphs <sup>c</sup>	Indirect	Mollusc: <i>Elysia crispata</i>
	Lecithotrophic	pelagic/benthic <sup>c</sup>	Indirect	Mollusc: <i>Elysia evelinae</i>
	Lecithotrophic	Among-population dimorphism and within-brood plasticity: Some populations show plastic dispersal, whereas others do not.	Indirect	Molluscs: <i>Haminoea zelandica</i> , <i>Elysia marcusii</i>
	Lecithotrophic	Seasonal dimorphism: Pelagic/benthic seasonal? (not clearly documented) <sup>d</sup>	Indirect	Mollusc: <i>Elysia timida</i>
	Lecithotrophic	Among-female dimorphism: Some females produce pelagic larvae and others have intracapsular metamorphosis with occasional variation within clutches.	Indirect	Mollusc: <i>T. pallida</i> (possibly poecilogony; planktotrophy has not been ruled out.)
Poecilogony <sup>e</sup>				
Nutritional dimorphism	Dimorphism: Females produce either planktotrophic or lecithotrophic (facultative?) larvae	Pelagic	Indirect	Mollusc: <i>Elysia zuleicae</i> , <i>Elysia pusilla</i> . Polychaete: <i>Streblospio benedicti</i>
	Plasticity: Females can switch between produce planktotrophic and lecithotrophic adelphophagic offspring	Pelagic	Indirect	Polychaete: <i>Polydora cornuta</i>
Nutritional and dispersal dimorphism	Plasticity: A single female can produce planktotrophic larvae, facultative lecithotrophic larvae, and lecithotrophic crawl-away juveniles.		Indirect	Mollusc: <i>Alderia willowi</i>
	Polymorphism: Populations produce either planktotrophic larvae or lecithotrophic crawl-away juveniles.		Indirect	Molluscs: <i>Costasiella ocellifera</i> , <i>Elysia chlorotica</i> . Polychaete: <i>Pygospio elegans</i>
	Polymorphism: Females produce either planktotrophic larvae or a mix of planktotrophic larvae and adelphophagic larvae.		Indirect	Polychaetes: <i>Boccardia proboscidea</i> , <i>Boccardia polybranchia</i> (?)

<sup>a</sup>Facultative planktotrophs fitting the restrictive criteria reviewed by Allen and Pernet (2007), and supplemented with Crump (1989).<sup>b</sup>Dispersal dimorphism reviewed in Krug (2009) and supplemented with Cumming (1993) and Carroll and Kempf (1990).<sup>c</sup>These reports remain unconfirmed as no details have been published and genetic or breeding data have not verified conspecific status.<sup>d</sup>Discussed in Krug et al. (2012b).<sup>e</sup>Details of poecilogony from Mackay and Gibson (1999); Krug (1998, 2009); Levin et al. (1991); Levin and Bridges (1994); Morgan et al. (1999); Gibson (1997); Gibson et al. (1999); Duchêne (1984); Oyarzun et al. (2011); Oyarzun and Strathmann (2011) and Vendetti et al. (2012).



**Fig. 2** Three scenarios for the evolution of intermediates in mode of development. *Scenario I*: Intermediates are necessary stages in the transition between two optimal modes of development. *Scenario II*: Intermediates are well adapted to a narrow range of conditions. *Scenario III*: All modes of development are equally adapted and transitions are relatively easy. (A) The inferred adaptive landscape. (B) The expected phylogenetic pattern. (C) The constraint imposed on evolution of mode of development by the evolutionary bias toward the loss of planktotrophic feeding larvae. Blue represents direct development, red planktotrophic development, and purple the intermediates discussed here.

both worlds (Emlet 1986). If intermediates are finely tuned to a narrow range of conditions, they should arise rarely but persist while the appropriate conditions exist (Hart 1996). Because evolutionary transitions in mode of development are biased toward the loss of planktotrophic larvae with a very low frequency of reversals and reacquisitions, intermediates may still be rare (Strathmann 1978a, b, 1995; Palumbi and Duda 1999). Under this scenario, branch lengths leading to intermediates should be similar to those observed for species with other modes of development, and they could show sister relationships with either direct developers or planktotrophs (Hart 1996). If the environmental conditions that select for intermediates persist for longer than the time necessary to speciate, intermediates could occur as small clades. A consistent position between basal planktotrophs and more derived direct developers would suggest that these intermediate forms play a role in facilitating evolutionary transitions between modes of development, or that speciation is itself associated with transitions in mode of development (Krug 2011); and

- (3) Finally, there is the possibility of a flat adaptive landscape, in which all modes of development have similar fitness (Scenario III in Fig. 2). In this case, intermediate forms should not be

particularly rare and are likely to occur in phylogenies in obviously transitional positions between direct developers and planktotrophs. They could also be found basal to transitions toward either of the other strategies. In this case, intermediates may appear at the base of adaptive radiations because they contain ample genetic variation for phenotypic plasticity, thereby setting the stage for genetic assimilation (West-Eberhard 2003; Schwander and Leimar 2011).

Simulation studies evaluating the range of speciation rates, relative probabilities of the different possible evolutionary transitions, and strength of association between changes in mode of development and speciation events are necessary to provide quantitative testable predictions of these scenarios.

### Phylogenetic placement of “intermediates”

All the kinds of intermediate forms discussed here are rare. Of the many hundreds of species in which mode of development has been observed and reported, facultative planktotrophy has been documented so far in only 8–22 species, depending on the criteria employed (Allen and Pernet 2007). Short-lived planktotrophic larvae that may retain

the potential to feed, but are so short lived that they are unlikely to benefit from feeding, represent only 5% of known calyptraeid development (Collin 2003). Thorson (1950) estimated that this kind of development occurs in only 5% of planktonic larvae. Dispersal polymorphisms have been reported for 11 species, all heterobranchs, and poecilogony has been verified for 10 species only from sacoglossan opisthobranchs and spionid polychaetes (Table 1) (Krug 2009). This rarity of intermediates indicates that mode of development is unlikely to evolve by sliding freely back and forth across a relatively flat adaptive landscape (Scenario III).

There are few species-level phylogenies of marine invertebrates in which the mode of development is known and in which an intermediate occurs. I found only one phylogeny including a poecilogonous species, three with a facultative planktotroph, and one with very short-lived planktotrophs (Table 2). The phylogeny of *Phestilla*, with its numerous changes between modes of development and very short branches leading to the facultative planktotroph *Phestilla sibogae* (Faucci et al. 2007), is consistent with Scenario I. The other phylogenies are consistent with Scenario II, and show no evidence that intermediates are unusually short-lived. In none of the groups have the intermediates speciated into small clades.

If sisters are likely to share the same mode of development, then speciation events occurring while conditions favor intermediates should result in small clades of intermediates. The absence of such small clades of intermediates suggest that either environmental conditions that select for intermediates do not persist long enough for speciation to occur or that sister species are not as likely to share a mode of development as we think. This could come about if shifts in mode of development are associated with speciation, implying that daughter species differ in their development (Krug 2011). This would generate at least one daughter species with one of the two common modes of development, while the intermediate mode of development could be retained in the other. More phylogenies, including species with intermediate development, are necessary before generalizations can be made about their role in evolutionary transitions of mode of development.

### How can environmental heterogeneity select for intermediates?

It is easy to imagine how intermediates can be lost. They can either go extinct or evolve into one of the two main types of development. Polymorphic

intermediates can be reduced by the loss of one morph, and developmental flexibility can be lost in the plastic or facultative intermediates. However, it is less easy to imagine how most intermediates, especially poecilogony, arise. The existing literature on the evolution of alternative phenotypes and bet-hedging can be employed to gain insights into the conditions that select for the evolution of intermediate modes of development. These intermediates could be used as interesting test cases of the hypotheses and models that have been put forward.

Spatial and temporal environmental heterogeneity have long been recognized as providing selection pressure for the evolution of alternative phenotypes (Moran 1992; West-Eberhard 2003). In the simple situation with two environments, as the frequency of either environment increases, the phenotype that matches the dominant environment is favored (Fig. 3A) (Moran 1992). When both environments occur at similar frequencies, plasticity is favored if the organisms are able to respond rapidly enough to accurate environmental cues and if costs are low (Fig. 3A) (Moran 1992). The poecilogonous sacoglossan *A. willowi* shows plasticity in mode of development that fits this model. In this slug, egg size and the mode of development track seasonal changes in temperature and salinity. This produces variation in development that appears to be an adaptation to the seasonal hydrological changes in the Californian estuaries where they live (Krug et al. 2012a). The temperature-mediated plastic response of hatching stage in *H. zealandiae* is another possible example (Clemens-Seely and Phillips 2011). Generalists are favored if accurate matching cannot be achieved (Fig. 3A) (Moran 1992). Facultative feeding larvae may represent this alternative generalist strategy, but they could also result from a bet-hedging strategy (see below). When the environment varies temporally, adaptive tracking is also a possible response (Simons 2011).

If genotypic and environmental cues act on a developmental system to produce the expressed phenotype, a slightly different breakdown of possible alternative phenotypes can be generated (Fig. 3B) (Leimar 2009). Similar to Moran's (1992) model, when both genetic and environmental cues have low accuracy, generalist or bet-hedging strategies are predicted, and when the accuracy of only the environmental cue is high, phenotypic plasticity is expected. When the genetic cue is accurate, genetic polymorphism or genetically polymorphic norms of reaction are expected (Leimar 2009). Although not explicitly considered by Leimar (2009), DNA methylation and other genetic modifications that can be transmitted as maternal

**Table 2** Phylogenetic position of intermediate modes of development

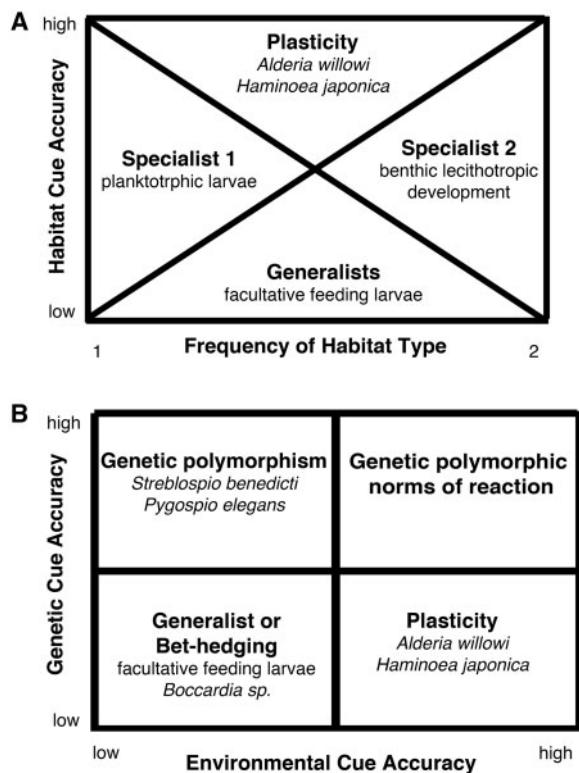
Group	Number of ingroup species in phylogeny	Between basal planktotrophs and derived direct developers	Between basal direct developers and derived planktotrophs	Among planktotrophs	Branch lengths	Reference
Molluscs						
Calyptraeids Short-lived planktotrophs	72	2	2	1	In 4/5 cases the branch leading to the intermediate is slightly longer than the sister.	Collin (2004)
<i>Conus</i>						
Facultative lecithotrophy	70	–	–	1	Branch length is slightly shorter than planktotrophic sisters	Palumbi and Duda (1999)
<i>Phestilla</i>						
Facultative lecithotrophy	6-8	–	–	Not yet reciprocally monophyletic with the sister planktotroph	Facultative lecithotroph is of very recent origin.	Faucci et al. (2007)
Echinoderms						
<i>Macrophiothrix</i>						
Facultative lecithotrophy	16	–	–	1	Similar to the two planktotrophic sisters	Hart and Podolsky (2005)
Polychaetes						
<i>Streblospio</i>						
Poecilogony	3	–	1	–	Similar to the two sisters	Mahon et al. (2009)

effects are likely to act in the same way as his genetic cues, without an actual change in the DNA sequence. Following this model, genetic polymorphism might be expected in *P. elegans* in which stable, among-population differences in mode of development occur throughout their range in the Baltic and North Seas (Kesäniemi et al. 2012). It is unknown whether the polymorphism is primarily genetic in this species. The different modes of development are, however, known to be genetically determined in *S. benedicti* (Levin et al. 1991; Levin and Bridges 1994), although their distribution relative to relevant environmental conditions is not well documented.

Unpredictable environmental fluctuations can favor bet-hedging over monomorphic generalists, plasticity, or genetic polymorphism (Sasaki and Ellner 1995; Leimar 2005; Simons 2011). Bet-hedging is a strategy that reduces variance in fitness and the risk of failure over the long term instead of maximizing immediate fitness (Philippi and Seger 1989; Haccou and Iwasa 1995; Sasaki and Ellner 1995; Simons 2011). This strategy is favored in unpredictable stochastic environments. Conservative bet-hedging is similar to “playing it safe” in which risk is uniformly reduced. Facultative feeding, where investment is

higher but development is successful regardless of the available resources, as well as the observation that most lecithotrophic eggs contain more resources than necessary for successful development (Allen and Pernet 2007) could both be explained as conservative bet-hedging strategies. By contrast, diversifying bet-hedging spreads the risk among an array of phenotypes. The packaging of two kinds of embryos in each capsule of *B. proboscidea* could result from individual females spreading the risk among their offspring. Diversifying bet-hedging could also explain the production of swimming and nonswimming hatchlings from the same egg mass or the production of larvae that settle in response to a specific cue and those from the same clutch that are nonselective (Krug 2001, 2009). Stochastic phenotype switching, a third kind of bet-hedging, is predicted to occur under a limited set of conditions (Kussell and Leibler 2005). The species, like *P. cornuta*, in which females have been observed to switch offspring type in the absence of any obvious environmental cue (MacKay and Gibson 1999) could be employing this strategy.

It is difficult to rigorously document bet-hedging traits because they are adaptive only over relatively



**Fig. 3** Conditions predicted to favor alternative phenotypes and some invertebrates that might fit each category. **(A)** The relationship between frequency of habitat type and accuracy of the environmental cue predicts the occurrence of phenotypic plasticity and of generalists (after Moran 1992). **(B)** The accuracy of the genetic cues versus environmental cues predict the occurrence of genetic polymorphism, plasticity, and bet-hedging (after Leimar 2009).

long timescales (Simons 2011), and the speculation that intermediates are hedging their bets needs to be empirically confirmed. Species like *B. proboscidea* that have short generation times and in which some females seem to hedge their bets by making two kinds of embryos while others produce only planktotrophs seems like an ideal species in which to examine long-term fitness of bet-hedging. Particularly interesting are the predictions that mixed-strategy bet-hedging should be more common than genetic polymorphism (Sasaki and Ellner 1995) and that bet-hedging should be more common than genetic polymorphisms in short-lived organisms (Seger and Brockmann 1987). In contrast to these predictions, mixed-strategy bet-hedging is known only from the two *Boccardia* species while the majority of poecilogonous species display polymorphisms. Sasaki and Ellner's Evolutionary Stable Strategy (ESS) model also predicts that the ESS of mixed-strategy bet-hedging is a population composed of females of a single genotype that divides offspring into several distinct morphs, instead of increasing continuous

variation within a brood. This is in contrast to *B. proboscidea* in which females with two different strategies, mixed-strategy bet-hedging and pure planktotrophy, co-exist (Oyarzun et al. 2011).

### Constraints on the evolution of alternative phenotypes

Since environmental variance of the kind expected to affect reproduction and development is almost ubiquitous in biological systems, it is perplexing that more alternative developmental phenotypes have not been reported. It is possible that they have been underreported due to hasty classification of development into one of the two traditional kinds, as has been suggested for facultative feeding larvae (Allen and Pernet 2007). It seems unlikely that mixed-strategy bet-hedging would be under-reported as examination of even a single female would result in the detection of multiple kinds of embryos. However, geographical or seasonal variation could be missed, as the development of many species has been reported for only a single location and field research is most often conducted in the summer months.

The rarity of intermediate modes of development may also reflect evolutionary constraints. The evolution of plasticity requires the ability to accurately detect the environmental cue, and respond appropriately in a timely manner (Moran 1992). With respect to variation in egg size, there is ample evidence that marine invertebrates can alter the sizes of their eggs or offspring in response to changes in environmental conditions such as temperature (Collin and Salazar 2010; Collin 2012) and competition (Allen et al. 2008). The only study to examine heritability of egg size in a marine invertebrate used selection experiments and half-sibling matings to detect significant heritability in *Hydroides elegans* worms (Miles et al. 2007; Miles and Wayne 2009). Most poecilogonous species produce the two modes of development via changes in the allocation of nurse eggs, extra-capsular yolk, or yolk vesicles. Plasticity and heritability of these extra-embryonic sources of nutrition have not been examined.

Accurate cues indicating environmental conditions are necessary for the evolution of plasticity and accurate genetic cues are necessary for the evolution of polymorphism. There is no reason to think that these are lacking in the marine environment or are any less reliable than in terrestrial systems. However, the speed with which egg size or extraembryonic yolk can be altered in response to environmental change could constrain the evolution of plasticity. Few data are available on this topic but work in my laboratory

indicates that temperature-mediated changes in egg size in *Crepidula* may have a significant time lag. As many as six brooding cycles are necessary after a change in temperature before the appropriate temperature-specific egg size is reached (Collin 2012). This lag may be sufficient to increase costs due to mismatches between phenotype and environment, and to result in selection against plasticity. Such a lag in response should not, however, prevent the evolution of diversified bet-hedging or polymorphisms. A better understanding of the physiological factors effecting sizes of eggs and offspring in marine invertebrates in general would be helpful in understanding potential constraints on the evolution of alternative developmental phenotypes.

### Summary

Species with intermediate modes of development, especially those that produce alternative phenotypes, are ideal systems with which to understand evolutionary transitions in mode of development in marine invertebrates. They also hold strong potential as model systems with which to test theories of the evolution of alternative phenotypes, and to understand the mechanisms underlying transitions between plasticity and polyphenism or polymorphisms (Schwander and Leimar 2011). However, detailed phylogenies need to be developed for most of the groups. The information available for each species is patchy; basic information about within-female and among-female variation, as well as geographical variation, is available for few species. Careful descriptions of the genetic and environmental factors influencing the expression of the different morphs will also need to be developed before most of these species can be fully utilized to test evolutionary theories. The collection of articles in this volume should stimulate the use of these unique species by pointing to productive directions for future inquiry.

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