

# The Biogeography of Marine Invertebrate Life Histories

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## Abstract

Biologists have long sought to identify and explain patterns in the diverse array of marine life histories. The most famous speculation about such patterns is Gunnar Thorson's suggestion that species producing planktonic larvae are rarer at higher latitudes (Thorson's rule). Although some elements of Thorson's rule have proven incorrect, other elements remain untested. With a wealth of new life-history data, statistical approaches, and remote-sensing technology, new insights into marine reproduction can be generated. We gathered life-history data for more than 1,000 marine invertebrates and examined patterns in the prevalence of different life histories. Systematic patterns in marine life histories exist at a range of scales, some of which support Thorson, whereas others suggest previously unrecognized relationships between the marine environment and the life histories of marine invertebrates. Overall, marine life histories covary strongly with temperature and local ocean productivity, and different regions should be managed accordingly.

## 1. INTRODUCTION

Geographical patterns in life-history traits such as body size, cell size, and maternal investment have inspired hypotheses for over a century of biological research (Allen 1877, Bergmann 1847, Moles & Westoby 2003, Thorson 1936). In the marine environment, identifying and understanding life-history patterns have a particular significance because of the otherwise bewildering array of modes of reproduction, developmental modes, and life histories in the sea (Strathmann 1985). Terrestrial life histories tend to map strongly to phylogeny, but marine life histories show tremendous variation that can be completely free of phylogenetic constraints. For example, congeners can vary from external fertilization with tiny long-lived, feeding larvae, to internal fertilization and no larval stage and very large offspring (Byrne 2006). Such variation demands exploration and explanation; so from the very beginning of marine larval studies, biologists have sought to identify patterns in life histories (for an excellent review, see Young 1990). Today, both managing and understanding our marine systems rely more than ever on the identification of patterns in life-history variation.

From an ecological perspective, the identification of geographical variation in marine life histories should lead to more effective management (Palumbi 2003). The ecological dynamics of any marine species is affected by its life history: Species with long-lived, far-dispersing larvae can have different population dynamics from species with short-lived larvae (Eckert 2003, Kinlan & Gaines 2003; but see Weersing & Toonen 2009). Similarly, species with highly dispersive larvae are likely to respond to natural and anthropogenic disturbances differently from species with larvae that spend only a few minutes in the water column (Levin 1984). If geographical variation in life histories exists, then management practices developed in one region may be inappropriate for another. For example, it has been suggested that the western coast of the United States is unusual for its preponderance of planktotrophic species (Goddard 1992). Much work on the spatial scales of connectivity in marine systems (e.g., Becker et al. 2007, Kinlan & Gaines 2003) and on marine life-history evolution (Strathmann 1987) comes from this region, but the generality of this research to other regions remains unclear.

From an evolutionary perspective, geographical patterns in life-history strategies may provide clues as to the selection pressures acting upon marine life histories (Thorson 1950). There has been much speculation on the advantages and disadvantages of a larval phase in marine organisms (Pechenik 1999; Strathmann 1974, 1993) and on whether mothers should produce many small larvae or a few large offspring (Smith & Fretwell 1974, Vance 1973). Although many attempts to address these problems have been made and progress has been steady, our understanding of the selection pressures that favor different strategies remains remarkably incomplete (Marshall & Morgan 2011). By identifying the conditions that are more commonly associated with some life-history strategies but not others, we may be able to infer how selection acts on reproduction and dispersal in the sea. For example, recent theory predicts that temperature should have a fundamental influence on marine invertebrate life histories (O'Connor et al. 2007) such that systematic variation among species across temperature gradients should be expected. Caution must be exercised, however. A genuine understanding of the evolutionary processes that generate macroevolutionary patterns must come from intraspecific studies (Bernardo 1996), and it must consider phylogenetic constraints (Collin 2004, Eckelbarger & Watling 1995, McHugh & Rouse 1998). For example, differential extinction or chance colonization events could drive spatial patterns in life history in apparently adaptive ways (Poulin & Feral 1996, Uthicke et al. 2009).

Perhaps the most famous speculation about the geography of marine life histories comes from the great Danish larval biologist Gunnar Thorson, who suggested that species from polar and deep-sea regions rarely, if ever, have planktonic development (Thorson 1936, 1946, 1950). He

suggested that “very limited periods of continuous phytoplankton production in connection with very low water temperatures” (Thorson 1950, p. 25) made conditions inhospitable to a larval phase. Because larvae are small and relatively vulnerable, the pelagic environment is a dangerous place (Morgan 1995). Thus, conditions that extend the larval period, low temperatures, or limited food likely increase larval mortality and select against a larval phase (O’Connor et al. 2007, Vance 1973). Thorson also suggested that species with pelagic, nonfeeding larvae were very rare and “constitute a rather small percentage of invertebrate species in temperate and warm seas, but are apparently absent from high-arctic seas” (Thorson 1946, p. 477). Importantly, most discussions of these ideas have centered on considering polar regions versus the rest of the world (Pearse 1994, Poulin & Feral 1996). Although Thorson certainly viewed polar regions as being particularly different, he also suggested that planktotrophy was much more common in the tropics than in temperate regions (Thorson 1946). Some of these ideas gathered widespread appeal, achieving paradigm status, and together they are sometimes referred to as “Thorson’s rule” (Mileikovsky 1975). Today, Thorson’s rule has less support (Pearse 1994). Indeed, it is now clear that species with pelagic larvae are present at both poles (Thorson believed species with pelagic larvae were absent from Antarctic waters) and in the deep sea (Clarke 1992, Pearse 1994). Perhaps the biggest problem with Thorson’s suggestions was that they were so absolute in nature—too often was the term “all” used in describing the patterns that he saw. Such language seems unwarranted given the likelihood of even one exception. Indeed, Thorson himself seemed troubled by the exceptions and noted that despite pelagic larvae being “suppressed” in the high arctic sea, some species with planktotrophic pelagic larvae “are among the most dominant animals of the high arctic coastal zones” (Thorson 1946, p. 434).

Over the ensuing ~70+ years, evidence accumulated that led opinions to shift against (or at least modify) Thorson’s rule. Both Young and Pearse give comprehensive accounts of the history of challenges and modifications to Thorson’s hypotheses (Pearse 1994, Young 1990). Suffice to say, evidence contradicting Thorson’s rule now seems so strong that Pearse suggested, “Thorson’s rule should be laid to rest, and Thorson should be remembered for his stimulating hypotheses that generated so many contributions in marine biology” (Pearse 1994, p. 26). It is now generally held that nonfeeding development predominates in both the poles and the deep sea, whereas more species produce feeding larvae in warm or temperate shallow waters (Clarke 1992, Pearse 1994, Pearse & Lockhart 2004). Since the 1990s, the biogeography of marine invertebrate life histories has been largely put aside (for some recent exceptions, see Collin 2003, Fernandez et al. 2009, Laptikhovskiy 2006, Poulin & Feral 1996), the matter now seemingly resolved and strong cautions against generalizations advised (Pearse 1994).

We believe, however, that there are now many reasons for revisiting the biogeography of reproduction in the sea. First, in the years since the last comprehensive global review (Emlet et al. 1987), a wealth of new data on the life history of marine invertebrates has accumulated (e.g., Anthes & Michiels 2007, Collin 2003, Fernandez et al. 2009, Kohn & Perron 1994, Marshall & Keough 2008a, McEdward & Miner 2001, Pearse 1994, Strathmann 1987, Wilson 2002), allowing a more comprehensive treatment of groups previously overlooked. Second, there have been few formal statistical treatments of marine invertebrate biogeography. Emlet et al. (1987) and Collin (2003) analyzed correlations between offspring size and latitude with linear regression and chi square tests, but for the most part, assessments of Thorson’s rule have lacked a formal statistical framework. Today, more targeted statistical approaches such as logistic regression are available that can directly address the relationship between developmental modes and latitude in a quantitative framework. Instead of viewing polar regions as “all or nothing” with regards to particular developmental modes, we can ask whether there is any statistically significant relationship between latitude and the distribution of alternative developmental modes. Recently,

Fernandez et al. (2009) used a more sophisticated statistical approach to model the molluscan and decapod species richness in different developmental modes along the coast of Chile to great effect. Third, latitude was used as a proxy for specific environmental variables because detailed biophysical data were previously unavailable. Thorson believed that both temperature and food availability decreased at higher latitudes and that one or both of these variables drove the patterns in marine invertebrate life histories (Thorson 1936, 1946); however, the poles are not foodless deserts as Thorson believed, and chlorophyll levels at any one time are not negatively correlated with latitude (see database available at <http://dx.doi.org/10.5061/dryad.m7j72>). Today, we can use remote sensing technology to directly test these hypotheses, using satellite imaging to estimate sea-surface temperatures and phytoplankton concentrations. Indeed, Collin (2003) used sea temperature data to examine latitudinal patterns in a group of gastropods. Fernandez et al. (2009) combined temperature data with chlorophyll *a* measurements to explore the biogeography of different developmental modes in molluscs and crabs along the Chilean coast and found that both temperature and productivity played a role in molluscs and anomuran crabs but not brachyuran crabs. With access to unprecedented levels of environmental data, more sophisticated statistical analyses, and a wealth of new life-history data, a re-examination of Thorson's rule should provide new insights into patterns of reproduction in the sea. For details of how we compiled life-history and environmental data and defined developmental groups and our analytical approach, see **Supplemental Text 1**. (Follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>.)

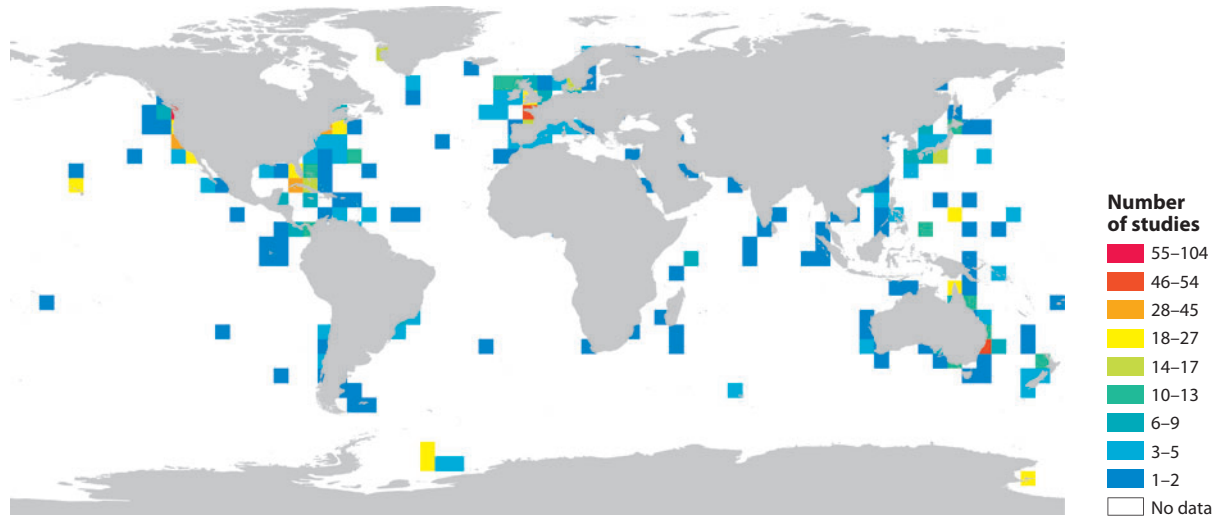
## 2. DISTRIBUTION OF DEVELOPMENTAL MODES ACROSS LATITUDES

Before discussing our findings, we should first acknowledge an important limitation of our meta-analysis. **Figure 1** shows that, despite the unprecedented size of our data set, it is extremely restricted geographically; most studies come from just a few, well-studied regions. Our findings are summarized in **Tables 1** and **2**. There is a higher fraction of aplanktonic species in the Southern Hemisphere than the Northern Hemisphere (north, 8%; south, 18%;  $\chi^2 = 26.2$ ,  $P < 0.001$ ), but of the species with planktonic larvae, identical fractions have feeding larvae (60%) in both hemispheres. The association between latitude and the fraction of species with planktonic larvae differs between hemispheres ( $\chi^2 = 27.8$ ,  $P < 0.001$ ). The fraction of aplanktonic species increases strongly with latitude in the south ( $\chi^2 = 36.6$ ,  $P < 0.001$ ), but if exclusively deep-water species are excluded, there is no relationship in the north (**Figure 2**). The latitudinal relationship also varies with phylum, indicated by a strong phylum  $\times$  latitude  $\times$  hemisphere interaction ( $\chi^2 = 20.7$ ,  $P < 0.001$ ), driven by a consistent lack of a relationship in the north but variation in the relationship among phyla in the south. Both southern echinoderms and molluscs show a strong relationship with latitude but no relationship is evident in annelids.

Of the species with pelagic larvae, a far lower fraction are feeding at higher latitudes ( $\chi^2 = 41.3$ ,  $P < 0.0001$ ) (**Figure 3**). This relationship is consistent between hemispheres (latitude  $\times$  hemisphere:  $\chi^2 = 0.022$ ,  $P = 0.882$ ) and among phyla (phylum  $\times$  latitude:  $\chi^2 = 0.23$ ,  $P = 0.627$ ), though the relationship appears strongest in molluscs and echinoderms.

## 3. VARIATION IN OFFSPRING SIZE AMONG DEVELOPMENTAL MODES ACROSS LATITUDES

As has been demonstrated repeatedly for different taxa, developmental mode is an excellent predictor of offspring size. Aplanktonic species produce the largest offspring, those with planktonic



**Figure 1**

A heat map of the distribution of studies used in this review to examine geographical variation in marine invertebrate life histories. Warmer colors indicate regions from which many species have been studied, cooler colors indicate areas from which only a few species have been studied, and white areas indicate areas from which we have no data. The vast majority of the marine environment remains unstudied, and our view of marine life histories comes from only a small fraction of those studies that exist. It should be noted that some areas are likely to have been studied, but these studies are largely inaccessible to the authors owing to language differences or limited accessibility.

nonfeeding larvae have intermediate offspring sizes, and those with feeding larvae have the smallest offspring sizes (**Figure 4**). Within planktonic species and those with nonfeeding larvae, offspring are generally larger in the Southern Hemisphere relative to the Northern Hemisphere, but species with feeding larvae are similar in size (**Figure 5**). The rank differences in offspring size among developmental modes were consistent across phyla (**Figure 4**), but within any developmental mode, there are significant differences in offspring size among phyla ( $F_{6,1091} = 34.3$ ,  $P < 0.001$ ). For example, among the planktonic species, echinoderm eggs were the largest and annelid eggs were the smallest; among the nonfeeding species, the eggs of echinoderms were again the largest, but mollusc eggs were the smallest.

**Table 1** Summary table of the relationship between the fraction of species with each development mode and various biophysical variables in marine invertebrates

	Aplanktonic	Planktonic nonfeeding	Planktonic feeding
Hemisphere	✓	×	×
Latitude	✓ (south only)	✓ (+)	✓ (-)
SST	✓ (-)	✓ (-)	✓ (+)
Ch a	✓ (-)	×	×
SST × Ch a	✓	×	×

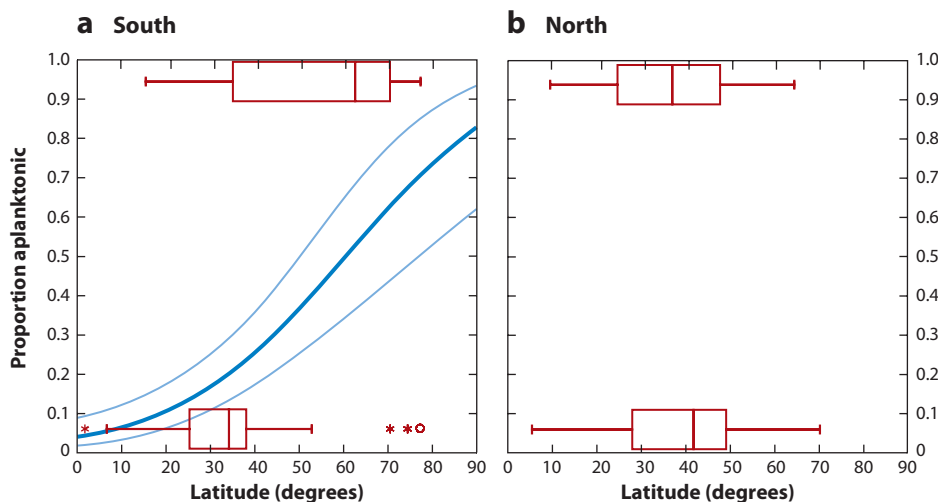
Key: Ticks, significant relationship; crosses, no relationship; - and +, negative or positive relationship between the predictor and response variable, respectively. Abbreviations: Ch a, chlorophyll a; SST, sea surface temperature.

**Table 2** Summary table of the relationship between offspring size and various biophysical variables in marine invertebrates

	Aplanktonic	Planktonic nonfeeding	Planktonic feeding
Hemisphere	✓	✓	×
Phylum	✓	✓	×
Latitude	✓ (+)	✓ (+)	✓ (+)
Sea surface temperature	✓ (-)	✓ (-)	✓ (-)
Chlorophyll a	×	✓ (-)	×

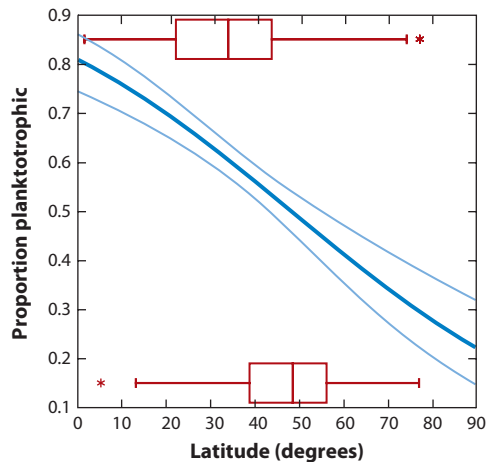
Key: Ticks, significant relationship; crosses, no relationship; – and +, negative or positive relationship between the predictor and response variable, respectively.

Offspring size increases with latitude across all developmental modes, but the relationship varies among modes ( $F_{2,1035} = 141.3$ ,  $P < 0.001$ ). The steepest relationship between offspring size and latitude occurred in aplanktonic species, and the shallowest relationship (though still significantly different from zero:  $P = 0.005$ ) occurred in species with feeding larvae (**Figure 6**). Although the relationship between offspring size and latitude was positive in all phyla, it varied in slope among phyla ( $F_{4,962} = 23.01$ ,  $P < 0.001$ ). The steepest relationships occurred in echinoderms and molluscs; among annelids the relationship was much weaker. Taxonomic class further influenced the relationship between latitude and offspring size (class  $\times$  latitude  $\times$  development mode:  $F_{10,953} = 28.3$ ,  $P < 0.001$ ); in fact, this interaction was driven by the lack of a relationship between latitude



**Figure 2**

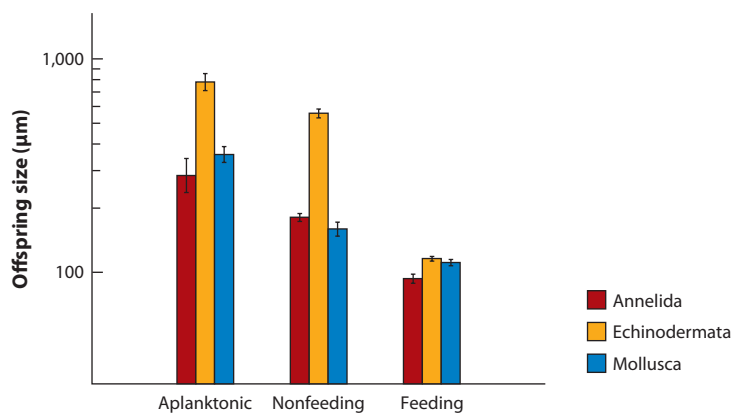
Proportion of species with aplanktonic development across latitude for (a) the Southern Hemisphere and (b) the Northern Hemisphere. There is no relationship between latitude and the prevalence of aplanktonic development in the Northern Hemisphere. The dark blue line indicates the line of best fit generated from a logistic regression, and light blue lines indicate upper and lower 95%-confidence intervals. Boxplots indicate the distribution of species across latitude in each developmental mode. Asterisks indicate points outside the interquartile range, and circles indicate points greatly outside of the interquartile range.



**Figure 3**

Proportion of species with planktonic development that have feeding larvae across latitude (pooled for both hemispheres). The dark blue indicates the line of best fit generated from a logistic regression, and light blue lines indicate upper and lower confidence intervals. Boxplots indicate the distribution of species across latitude in each developmental mode. Asterisks indicate points outside the interquartile range.

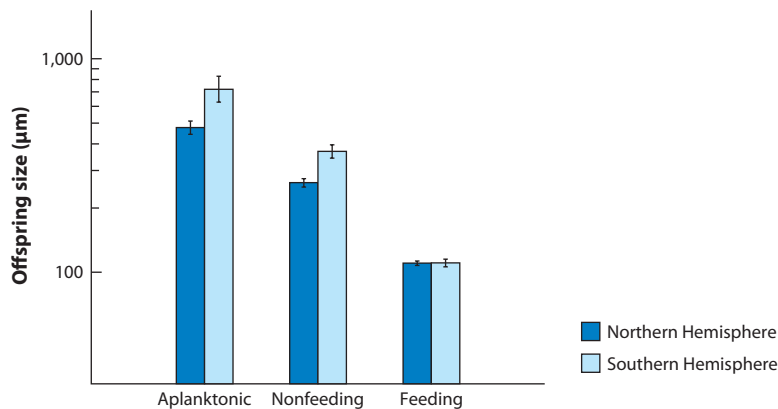
and offspring size in holothuroids and ophiuroids but by more complex associations in polychaetes. In polychaetes, there is a weak, but significantly positive relationship between latitude and offspring size, but this relationship varies in slope between hemispheres (latitude  $\times$  hemisphere:  $F_{1,228} = 8.43$ ,  $P = 0.004$ ). There is a strong, positive relationship between latitude and offspring size in all developmental modes in the Southern Hemisphere polychaetes ( $F_{1,34} = 6.008$ ,  $P = 0.02$ ), but for Northern Hemisphere polychaetes, the relationship is marginally nonsignificant ( $F_{1,194} = 2.87$ ,  $P = 0.09$ ).



**Figure 4**

The size of offspring (estimated as egg diameter) from three developmental modes across the three phyla (Annelida, Echinodermata, and Mollusca) for which we have the most complete data. Each bar indicates the mean ( $\pm$  standard error) offspring size for each developmental mode. Note the y-axis shows a  $\log_{10}$  scale.





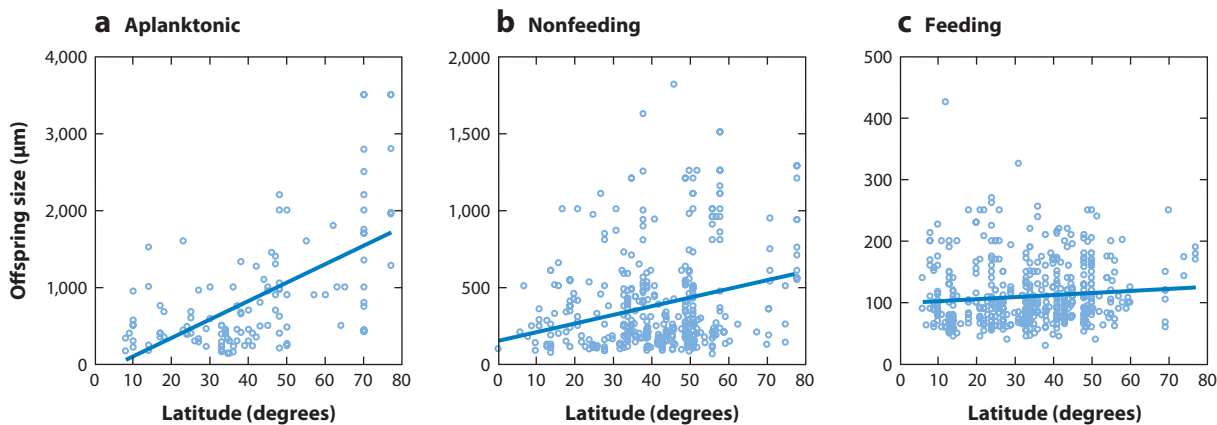
**Figure 5**

The size of offspring from three developmental modes across two hemispheres. Each bar indicates the mean ( $\pm$  standard error) offspring size for each developmental mode. Note the  $y$ -axis shows a  $\log_{10}$  scale.

#### 4. REGIONAL EFFECTS

The use of ANCOVA (analysis of covariance) accounts for the effect of latitude, but there were still regional differences in the relative fractions of each developmental mode and in egg sizes (excluding regions that spanned a narrow range of latitudes such as the Caribbean and Antarctica). There were strong region  $\times$  latitude interactions affecting the fraction of species with pelagic larvae ( $\chi^2 = 5.03$ ,  $P = 0.025$ ) and the fraction of larvae that were feeding ( $\chi^2 = 7.25$ ,  $P = 0.007$ ). For both response variables, latitudinal gradients in developmental mode were much steeper in Australia than in North America, and these regions appeared to drive much of the interaction.

There were also regional differences in egg size within developmental modes. Offspring size differed among regions for species with planktotrophic larvae ( $F_{5,453} = 7.85$ ,  $P < 0.001$ ) and



**Figure 6**

The relationship between offspring size (estimated as egg diameter) and latitude for each developmental mode. Each point represents the mean of individual species and the dark blue line indicates the line of best fit from a linear regression. Panels show (a) the relationship for species with aplanktonic development, (b) the relationship for species with nonfeeding larvae, and (c) the relationship for species with feeding larvae. Note that in all three developmental modes, there is a significantly positive relationship between offspring size and latitude.



also for species with pelagic lecithotrophic development ( $F_{5,315} = 3.81$ ,  $P = 0.002$ ). The largest nonfeeding larvae are in Australia (mean size = 480  $\mu\text{m}$ ), and the smallest nonfeeding larvae are in North America (mean size = 250  $\mu\text{m}$ ). The largest feeding larvae are in South America (mean size = 145  $\mu\text{m}$ ), and the smallest feeding larvae are in Australia (mean size = 90  $\mu\text{m}$ ). There was no influence of region on egg size in aplanktonic species.

## 5. THE ROLE OF EXTREMES: EXCLUDING THE POLES AND/OR THE TROPICS

The latitudinal patterns of developmental modes are largely unaffected by whether we include the poles and the tropics. Excluding neither the poles ( $>60^\circ$ ) nor the tropics ( $<30^\circ$ ) has no effect on the pattern of higher fractions of aplanktonic species at higher latitudes. Similarly, the relationship between the prevalence of species with feeding larvae and latitude remains regardless of whether the tropics and poles are included.

Within each developmental mode, trends in offspring size were also fairly robust to the influence of low and high latitudes. When the tropics were excluded, there was still a strong positive association between offspring size and latitude across all developmental modes. When the poles were excluded (both with and without the tropics), the relationships between offspring size and latitude remain for aplanktonic species and species with nonfeeding larvae, but was not detected in species with feeding larvae.

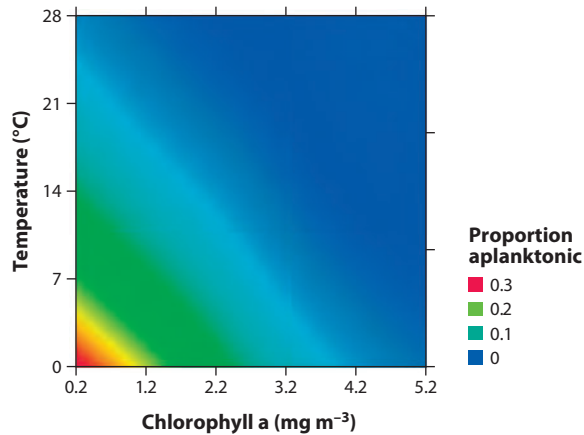
## 6. THE ROLE OF SEA SURFACE TEMPERATURE AND OCEAN PRODUCTIVITY

There is a strong association between the prevalence of each developmental mode and local temperature and productivity. The fraction of species with aplanktonic development varied with both temperature and chlorophyll concentration (chlorophyll  $\times$  temperature:  $\chi^2 = 7.22$ ,  $P = 0.007$ ). Lower temperatures were associated with less planktonic development, and this association was stronger at low productivity levels (**Figure 7**): Planktonic larvae were more common where both temperature and productivity were high, whereas areas with the lowest productivity and temperature had the most aplanktonic species. The fraction of species with feeding larvae increased with temperature ( $\chi^2 = 27.0$ ,  $P < 0.001$ ) but not with productivity ( $\chi^2 = 0.77$ ,  $P = 0.381$ ).

Within each developmental mode, the relationship between temperature, productivity, and offspring size is variable (developmental mode  $\times$  temperature:  $F_{2,809} = 109.9$ ,  $P < 0.0001$ ; developmental mode  $\times$  chlorophyll:  $F_{2,809} = 4.76$ ,  $P = 0.009$ ). In aplanktonic species or species with feeding larvae, as temperature increases, offspring size decreases (aplanctonic:  $t_{87} = 8.23$ ,  $P < 0.001$ ; feeding:  $t_{408} = 3.37$ ,  $P = 0.001$ ). In species with nonfeeding larvae, larger offspring sizes were associated with lower temperatures and also with lower levels of productivity (temperature:  $t_{315} = 5.35$ ,  $P < 0.001$ ; chlorophyll:  $t_{315} = 3.17$ ,  $P = 0.002$ ; **Figure 8**).

## 7. PHYLOGENETICALLY CONTROLLED ANALYSES

For 83 species of sacoglossan sea slugs, evolutionary history had little effect on the patterns we saw. Model fit did not improve when development mode and latitude were allowed to covary (**Supplemental Table 1**), supporting a model of uncorrelated trait evolution and indicating that lecithotrophic species were not more abundant in the tropics. Models of egg-size evolution with no phylogenetic correction ( $\lambda = 0$ ) were preferred over models in which  $\lambda$  was jointly estimated

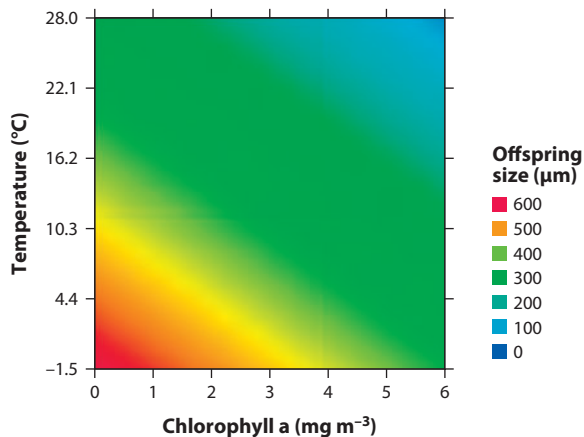


**Figure 7**

The relationship between the proportion of species showing aplanktonic development and the average sea surface temperature and chlorophyll a levels in the region in which the species was studied. The figure shows a heat plot for the plane of best fit generated from logistic multiple regressions, where warmer colors indicate a higher proportion of species with aplanktonic development and cooler colors indicate a lower proportion of species with aplanktonic development. When temperatures are warmer and food availability is greater, planktonic development is more common.

(log-BF test = 3.7), indicating no phylogenetic effect on egg size exists in this group. Among species with lecithotrophic development, there was a significant and positive relationship between egg size and latitude even when correcting for phylogenetic effects (**Supplemental Table 1**). There was no relationship between egg size and latitude for planktotrophic sacoglossans.

For 40 species of Calyptraeid gastropods, phylogenetic effects were more pronounced. There was no latitudinal pattern in the distribution of development modes (**Supplemental Table 1**).



**Figure 8**

The relationship between offspring size and average sea surface temperature and chlorophyll a levels in the region in which the species was studied for species with nonfeeding larvae. The figure shows a heat plot for the plane of best fit generated from multiple regressions, where warmer colors indicate larger offspring sizes and cooler colors indicate smaller offspring sizes. When temperatures are cooler and food availability is lower, offspring tend to be larger.

Models of egg-size evolution that included a phylogenetic correction were strongly preferred over models in which  $\lambda = 0$  (log-BF test = 12.1), indicating a strong phylogenetic effect. In contrast to the overall pattern for molluscs, planktotrophic egg size was significantly but negatively correlated with latitude (**Supplemental Table 1**); however, this relationship was apparent with or without the phylogenetic correction. There was no correlation between lecithotrophic egg size and latitude.

## 8. DISCUSSION

The geographic distributions of the life histories of marine invertebrates differ greatly between the Northern and Southern Hemispheres. The Northern Hemisphere is characterized by low levels of aplanktonic development and much smaller offspring sizes within aplanktonic and nonfeeding pelagic species. The Southern Hemisphere has twice as many aplanktonic species as the Northern Hemisphere and also appears to show much stronger latitudinal trends than the Northern Hemisphere. The increase in the fraction of aplanktonic species at higher southern latitudes could be explained by the general idea that Thorson put forward, that the cold Antarctic waters would be inhospitable to larvae; but it should be remembered that ~20% of the species in the Antarctic have a larval phase, and in the Arctic, more than 70% of species have a larval phase. Our finding of stronger latitudinal patterns in the Southern Hemisphere relative to the Northern Hemisphere echoes earlier work on echinoids and asteroids (Clarke 1992, Emlet et al. 1987, Pearse 1994). It appears that, for a range of phyla, Thorson's idea that species with planktonic larvae are rarer at high latitudes only applies in the Southern Hemisphere. Why there should be a significant relationship in the south but no relationship in the north is unclear—differences in phylogeny, evolutionary history, or oceanography could drive patterns at this scale. We suspect that a combination of oceanography and differences in the representation of higher latitudes among hemispheres drove this pattern. Boundary currents moving along the edges of ocean basins carry water from different latitudes along the coast, reducing the latitudinal effect on temperature (and therefore, presumably offspring size) in some places. In the Northern Hemisphere, boundary currents and the (relatively) poor sampling of very high latitudes resulted in a smaller temperature range being sampled than in the Southern Hemisphere. Thus, latitude is a poorer proxy for temperature in the north than the south in our data set ( $R^2$  for latitude-temperature relationship in the north = 0.913, and south = 0.949). Importantly, when temperature, rather than latitude, was used as a predictor for the prevalence of planktonic species, we found no differences between hemispheres. Thorson's suggestion that planktotrophy is rarer at the poles does stand the test of time: In both hemispheres, there is a marked decrease in the fraction of species with feeding larvae at higher latitudes.

Thorson's predictions were less accurate for species with nonfeeding larvae. As noted elsewhere (Clarke 1992, Pearse 1994), there is a marked increase in species with pelagic nonfeeding larvae moving from the equator to the poles. This is in stark contrast with Thorson's assertion that pelagic nonfeeding larvae were absent from the poles, a notion that troubled him: "...that lecithotrophic larvae seem to be totally absent. . . seems at first to be the opposite of what might be expected. At the outset it would seem that precisely this type of larval development. . . would be well fit for the life in arctic seas" (Thorson 1946, p. 437). As Thorson intuited, the majority of species in the poles indeed do have nonfeeding larvae. More generally, we were surprised by the high fraction of species with nonfeeding larvae: In both hemispheres, 40% of species with planktonic larvae have lecithotrophic development. If we were to include phyla such as sponges and bryozoans (i.e., those with almost exclusively nonfeeding larvae), this fraction would be much higher, suggesting that nonfeeding larval development is the dominant mode of reproduction in coastal marine invertebrates.

Prior consideration of Thorson's predictions and ensuing discussions of latitudinal patterns (Clarke 1992, Pearse 1994, Poulin & Feral 1996) focused largely on patterns driven by the poles

(but see Collin 2003, Emler et al. 1987). However, our analyses support a more nuanced view of how life-history strategies are distributed across the globe. As Thorson first suggested, there are also patterns in temperate and tropical seas: Both pelagic development and feeding larvae are rarer at higher latitudes (Thorson 1946, 1950). This pattern exists even when considering only the temperate latitudinal band of 30°–60°. Thus, planktonic development and planktotrophy both decrease in prevalence moving poleward, but this pattern is not driven solely by adaptation to the extreme environment of the polar oceans. These latitudinal patterns within the temperate band are perhaps not surprising given similar intraspecific patterns in offspring size (Marshall et al. 2008). Overall, it seems that we must not only account for variation in reproduction and development between the poles and the rest of the world, but also within temperate regions.

It is difficult to account for the differences in offspring sizes between hemispheres. Temperatures for a given latitude are generally cooler in the Southern Hemisphere, but only slightly. Interestingly, the differences in offspring size among hemispheres were restricted to species with nonfeeding larvae, which suggests that simple temperature effects may not explain the differences. Based on the biophysical data included in our analyses, the Southern Hemisphere is also less productive than the Northern Hemisphere (Northern Hemisphere productivity is largely driven by the productive western coast of the US and the limited representation of the productive South American coast in our data set) (**Figure 1**). Southern Hemisphere mothers may, therefore, provide higher levels of provisioning for their offspring to offset the lack of food available to offspring. Alternatively, phylogenetic effects could be driving the differences in offspring size among hemispheres.

The inclusion of biophysical variables in our analyses provided key insights into marine life-history patterns. As we expected, there was a strong negative relationship between offspring size and temperature. Physiologists have long recognized that temperature affects many life-history traits, including offspring size (Von Bertalanffy 1960, Woods 1999). It could be that the patterns in offspring size we observed with temperature are simple physiological side effects of cooler temperatures (Bownds et al. 2010, Fischer et al. 2003, Van der Have & de Jong 1996). Van der Have & de Jong (1996) showed that, because growth (cell size increases) and differentiation (cell number increases) rates are differentially affected by temperature, larger sizes at metamorphosis are inevitable. How these physiological processes affect offspring size in marine invertebrates remains unclear, but we suspect that the pattern is driven by more than simple physiology given that the relationship between temperature and offspring size was so variable among developmental modes. Furthermore, the few intraspecific studies that have examined temperature-induced offspring size changes in marine invertebrates and fish suggest that they do indeed have an adaptive basis (Bownds et al. 2010, Burgess & Marshall 2011, Salinas & Munch 2012). Nevertheless, we suggest that future studies examine the complex interplay between temperature, development, and offspring size to delineate the role of physiological processes in generating these patterns (Van der Have & de Jong 1996).

Perhaps the most exciting result of our meta-analysis is the combined associations of temperature and productivity with marine invertebrate life-history patterns. Thorson was incorrect in assuming that the polar waters are completely food limited, but he was correct in thinking that both temperature and food influence the incidence of planktonic development. Our results in this regard are intuitively appealing: Planktonic larvae are more common when food levels and temperature are high, and these are conditions that allow rapid development and, hence, minimize larval mortality due to advection, predation, and starvation (Morgan 1995, Vance 1973). The interaction between temperature and productivity (and by inference, larval food) is particularly interesting: For a given temperature, planktonic development is more common under conditions of lower productivity. A surprising result was that food affects the fraction of species with free-swimming

pelagic larvae but not the incidence of planktotrophy; this finding suggests that productivity affects selection on the presence of a larval phase but not on larval feeding. This finding is in contrast to that of Fernandez et al. (2009), where productivity affects the species richness of planktotrophic molluscs and anomuran species along the Chilean coast. Our measure of productivity was very coarse; however, based on mean productivity across two summer and two winter months. Future studies of more fine-scale estimates of productivity should provide further insight into how it shapes marine life histories.

Our meta-analysis showed that in species with nonfeeding larvae, lower levels of productivity are associated with much larger offspring sizes. Differences in productivity have previously been implicated in shifts in offspring size and developmental mode over evolutionary time (Uthicke et al. 2009). For example, the rise of the Panamanian Isthmus resulted in high levels of productivity on the Pacific side and low levels in the Caribbean. In geminate pairs of bivalves and echinoderms, Pacific species produced much smaller eggs compared to species in the nutrient-poor Caribbean (Lessios 1990, Moran 2004).

We found no overall effect of phylogeny on egg size in sacoglossan sea slugs, but there was a strong influence of phylogeny on Calyptraeid egg sizes. The lack of phylogenetic effect is perhaps not surprising given the frequent evolutionary transitions between development modes in sacoglossans (Krug 2009). The effect estimated for Calyptraeidae contrasts with results by Collin (2004), who found no such effect; differences in methodology (Markov chain Monte Carlo versus maximum likelihood) or phylogenetic resolution may explain the different outcomes. In each group, however, patterns within a development mode were detectable with or without a phylogenetic correction. Latitude was positively related to egg size for lecithotrophic sacoglossans but was negatively correlated with egg size for planktotrophic Calyptraeidae. These trends were seen in conventional statistical analyses of each group and were unaffected by inclusion of a formal phylogenetic correction in models of trait evolution, suggesting that the trends we report from the full data set are not artifacts of shared history within groups. More comparative studies are clearly needed to identify clades like the Calyptraeidae and *Comus*, within which trends run counter to those described for the rest of a given phylum; such exceptions may prove useful in identifying causal factors that drive trends in egg size. Overall, our efforts to include phylogenetic analyses were hampered by a poor overlap between those species for which we have life-history data and those species for which molecular phylogenies exist, highlighting a need for future efforts to bridge this gap.

## 9. SELECTION ACROSS THE LIFE HISTORY

Thorson and subsequent investigators sought to explain marine life-history patterns by focusing on selection acting on planktonic larvae (but see Havenhand 1995, Marshall & Morgan 2011). However, selection across the entire life history must be considered to advance our understanding of how larval strategies evolve. High planktonic mortality rates certainly impose strong selection on larvae, but so too must forces acting on pre- and postlarval stages (Marshall & Morgan 2011, Roughgarden 1989). Within a species, offspring size-specific selection can act at both fertilization and postmetamorphic performance (Marshall & Keough 2008a). More generally, organisms with complex life cycles are likely to express traits that are the product of complementary and conflicting selection pressures across the entire life history (Schluter et al. 1991). Multiple lines of evidence in our meta-analysis suggest that environmental influences on multistage selection may be responsible for interspecific variation in offspring size in marine invertebrates that we observed, and below we outline each.

The relationship between offspring size and temperature was not consistent among developmental modes and was steepest in two modes in which no larval feeding takes place. If simple

physiological effects drove the relationship between temperature and offspring size, it seems reasonable to expect similar slopes across all developmental modes. Because species with feeding larvae occupy a narrower band of egg sizes, this group may simply be more constrained with regard to the slope of the relationship between temperature and offspring size. One theory predicts metamorphosis should be more costly at cooler temperatures (Rombough 2006), but this idea remains untested in marine invertebrates and should be explored. Alternatively, selection for increased size postmetamorphosis may be stronger in cooler temperatures. In species with no larval feeding stage, there is a positive association between egg size and size at metamorphosis (Collin 2003, Emler et al. 1987). As noted by several other researchers (Emler et al. 1987, Pearse et al. 1991), nonfeeding larvae can complete metamorphosis coming from eggs smaller than 200 microns, and so any increase in offspring size beyond this may be used solely to increase performance and resilience postmetamorphosis. We saw a strong association between offspring size and temperature in species with no larval stage and in species with nonfeeding larvae, suggesting that selection favors larger juveniles at lower temperatures. Although this is an intriguing hypothesis, only one study has formally examined selection on offspring size across a latitudinal gradient. Marshall & Keough (2008b) found postmetamorphic selection favored larger offspring at higher latitudes, but the effect of latitude was not due solely to temperature: Selection actually favored smaller offspring in winter than summer. We therefore echo earlier calls (Havenhand 1995, Pearse et al. 1991, Wray 1995) for studies that formally examine variability in postmetamorphic selection on offspring size across environmental gradients.

Productivity affected offspring size in species with nonfeeding larvae; lower levels of productivity resulted in larger offspring sizes in this group. Many studies within species show that mothers that experience limited food often produce larger offspring because selection for increased offspring size intensifies when food is scarce (Allen et al. 2008, Bashey 2006, Fox et al. 1997). In areas with lower productivity, presumably food availability is lower (particularly for filter feeders that rely on phytoplankton), and in these areas, mothers may produce larger eggs in order to compensate for poorer food conditions that their offspring will encounter postmetamorphosis (Allen et al. 2008, Fox et al. 1997). This explanation assumes that lower productivity as measured by chlorophyll *a* is a good predictor of food availability more generally: This assumption will be more appropriate for some species than others. The pattern of larger offspring in species with nonfeeding larvae in conditions of lower productivity is repeated at the regional scale: Adjusted for latitude, North America has the highest measures of chlorophyll *a*, whereas Australia has the lowest. These regions were also the site of the smallest and largest nonfeeding larvae, respectively. To test the hypothesis that lower food availability selects for larger size at metamorphosis, formal tests across naturally varying food gradients or experimental manipulations are required (Fox et al. 1997).

## 10. MANAGEMENT IMPLICATIONS

Our results are relevant for managers: The life histories of marine invertebrates vary predictably among regions and along latitudinal gradients, and different regions should be managed accordingly (Kelly & Eernisse 2007, O'Connor et al. 2007). For most benthic animals, larval development mode determines the spatial scale of migration among demes. Understanding larval connectivity is thus critical for spacing of marine protected areas to ensure genetic and demographic exchange among reserves and replenishment of adjacent areas (Botsford et al. 2001, Palumbi 2003, Shanks et al. 2003, White et al. 2010). A mismatch between the typical larval dispersal kernel and the spacing of marine reserves can threaten population persistence and recolonization dynamics on ecological timescales (Hastings & Botsford 2006). Differences in life-history patterns among



regions and latitudes may drive predictable changes in connectivity among reserves, particularly across latitudinal bands; higher latitudes are poor in species with dispersive, feeding larvae, thus high-latitude reserves may experience reduced connectivity compared to tropical regions. Such predictions are overly simplistic, however; for example, nonfeeding larvae that develop in extreme cold can have longer pelagic durations than feeding larvae developing in warm tropical waters (Pearse et al. 1991). On balance, however, we expect cooler regions to have more poorly connected populations than the tropics owing to the increased fraction of species with planktonic and nonfeeding larvae. Note that our expectation, at first glance, seems to contradict that of O'Connor et al. (2007), who suggested that, all being equal, connectivity should be greater at the poles relative to the tropics because developmental rates are much faster in the tropics. The conclusions of O'Connor et al. (2007) certainly hold for any one developmental mode: Within each developmental mode, we would expect greater connectivity among distant populations in poles relative to the tropics because of slower developmental rates in cooler clines. Overall, however, because of the differences in representation of different developmental modes across latitudes, we would expect a higher fraction of dispersive, planktotrophic species in the tropics relative to the poles and, therefore, greater connectivity at lower latitudes.

Connectivity is not the only ecological process relevant to management that is likely to be affected by life history; there is some evidence that population variability may also be affected. Eckert (2003) showed that species with planktonic development tend to show more variation in abundance over time relative to species with a larval stage. If this pattern applies globally, our results suggest that, because low-temperature regions (as well as places with very low productivity) have more species with planktonic development, populations in these regions should exhibit more variability over time and should be managed accordingly.

Our findings have implications for how anthropogenic climate change may affect species distributions in the future. We found that species with planktotrophic development were more common in warmer conditions and that offspring were smaller at higher temperatures across all developmental modes. Assuming that temperature is the causal factor driving these relationships, we might expect that as global temperatures increase with climate change, species with planktotrophic development (and smaller eggs more generally) will become more common. Conversely, we might expect species with nonfeeding larvae to become less common worldwide. Furthermore, we might expect species with planktotrophic development to show range expansions toward the poles and contraction of the ranges of species with nonfeeding toward the poles. Already, the range shifts of some planktotrophic species have been linked to climate change (Ling et al. 2009). Further tests examining the direct effect of temperature on the selective advantage of different developmental modes and offspring sizes are therefore urgently needed.

## DISCLOSURE STATEMENT

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Richard Fuller assisted in the preparation of **Figure 1**. This paper is dedicated to the memory of Leonard George Drennan (April 1, 1927–November 24, 2011).

## LITERATURE CITED

- Allen JA. 1877. The influence of physical conditions in the genesis of species. *Radic. Rev.* 1:108–40
- Allen RM, Buckley YM, Marshall DJ. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.* 171:225–37
- Anthes N, Michiels NK. 2007. Reproductive morphology, mating behavior, and spawning ecology of cephalaspid sea slugs (Aglajidae and Gastropteridae). *Invertebr. Biol.* 126:335–65
- Bashey F. 2006. Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* 60:348–61
- Becker BJ, Levin LA, Fodrie FJ, McMillan PA. 2007. Complex larval connectivity patterns among marine invertebrate populations. *Proc. Natl. Acad. Sci. USA* 104:3267–72
- Bergmann C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Stud.* 3:595–708
- Bernardo J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* 36:216–36
- Botsford LW, Hastings A, Gaines SD. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* 4:144–50
- Bownds C, Wilson RS, Marshall DJ. 2010. Why do colder mothers produce larger eggs? An optimality approach. *J. Exp. Biol.* 213:3796–801
- Burgess SC, Marshall DJ. 2011. Temperature-induced maternal effects and environmental predictability. *J. Exp. Biol.* 214:2329–36
- Byrne M. 2006. Life-history diversity and evolution in the Asterinidae. *Integr. Comp. Biol.* 46:243–54
- Clarke A. 1992. Reproduction in the cold: Thorson revisited. *Inv. Repro. Dev.* 22:175–84
- Collin R. 2003. Worldwide patterns in mode of development in calyptraeid gastropods. *Mar. Ecol. Progr. Ser.* 247:103–22
- Collin R. 2004. Phylogenetic effects, the loss of complex characters, and the evolution of development in calyptraeid gastropods. *Evolution* 58:1488–502
- Eckelbarger KJ, Watling L. 1995. Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates. *Invertebr. Biol.* 114:256–69
- Eckert GL. 2003. Effects of the planktonic period on marine population fluctuations. *Ecology* 84:372–83
- Emlet RB, McEdward LR, Strathmann RR. 1987. Echinoderm larval ecology viewed from the egg. In *Echinoderm Studies*, ed. M Langoux, J Lawrence, pp. 55–136. Rotterdam: A.A. Balkema
- Fernandez M, Astorga A, Navarrete SA, Valdovinos C, Marquet PA. 2009. Deconstructing latitudinal species richness patterns in the ocean: Does larval development hold the clue? *Ecol. Lett.* 12:601–611
- Fischer K, Brakefield PM, Zwaan BJ. 2003. Plasticity in butterfly egg size: Why larger offspring at lower temperatures? *Ecology* 84:3138–47
- Fox CW, Thakar MS, Mosseau TA. 1997. Egg size plasticity in a seed beetle: an adaptive maternal effect. *Am. Nat.* 149:149–63
- Goddard JHR. 1992. *Patterns of Development in Nudibranch Molluscs from the Northeast Pacific Ocean, with Regional Comparisons*. Eugene, Oregon: Univ. Or. Press
- Hastings A, Botsford LW. 2006. Persistence of spatial populations depends on returning home. *Proc. Natl. Acad. Sci. USA* 103:6067–72
- Havenhand JN. 1995. Evolutionary ecology of larval types. In *Ecology of Marine Invertebrate Larvae*, ed. LR McEdward, pp. 79–122. Boca Raton: CRC
- Kelly RP, Eernisse DJ. 2007. Southern hospitality: a latitudinal gradient in gene flow in the marine environment. *Evolution* 61:700–7
- Kinlan BP, Gaines SD. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–20
- Kohn AJ, Perron FE. 1994. *Life-History and Biogeography Patterns in Conus*. Oxford: Clarendon. 106 pp.

- Krug PJ. 2009. Not my “type”: larval dispersal dimorphisms and bet-hedging in opisthobranch life histories. *Biol. Bull.* 216:355–72
- Laptikhovskiy V. 2006. Latitudinal and bathymetric trends in egg size variation: a new look at Thorson’s and Rass’s rules. *Mar. Ecol.* 27:7–14
- Lessios HA. 1990. Adaptation and phylogeny as determinants of egg size in echinoderms from the two sides of the Isthmus of Panama. *Am. Nat.* 135:1–13
- Levin LA. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology* 65:1185–200
- Ling SD, Johnson CR, Ridgway K, Hobday AJ, Haddon M. 2009. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Glob. Chang. Biol.* 15:719–31
- Marshall DJ, Allen RM, Crean AJ. 2008. The ecological and evolutionary importance of maternal effects in the sea. *Oceanogr. Mar. Biol. Annu. Rev.* 46:203–50
- Marshall DJ, Keough MJ. 2008a. The evolutionary ecology of offspring size in marine invertebrates. *Adv. Mar. Biol.* 53:1–60
- Marshall DJ, Keough MJ. 2008b. The relationship between offspring size and performance in the sea. *Am. Nat.* 171:214–24
- Marshall DJ, Morgan SG. 2011. Ecological and evolutionary consequences of linked life-history stages in the sea. *Curr. Biol.* 21:R718–25
- McEdward LR, Miner BG. 2001. Larval and life-cycle patterns in echinoderms. *Can. J. Zool.* 79:1125–70
- McHugh D, Rouse GW. 1998. Life history evolution of marine invertebrates: new views from phylogenetic systematics. *Trends Ecol. Evol.* 13:182–86
- Mileikovsky SA. 1975. Types of larval development in Littorinidae (Gastropoda: Prosobranchia) of the world ocean, and ecological patterns of their distribution. *Mar. Biol.* 30:129–35
- Moles AT, Westoby M. 2003. Latitude, seed predation and seed mass. *J. Biogeogr.* 30:105–28
- Moran AL. 2004. Egg size evolution in tropical American bivalves: the fossil record and the comparative method. *Evolution* 58:2718–33
- Morgan SG. 1995. Life and death in the plankton: larval mortality and adaptation. In *Ecology of Marine Invertebrate Larvae*, ed. L McEdward, pp. 279–322. Boca Raton: CRC
- O’Connor M, Bruno JF, Gaines SD, Halpern BS, Lester SE, et al. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc. Natl. Acad. Sci. USA* 104:1266–71
- Palumbi SR. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* 13:S146–58
- Pearse JS. 1994. Cold-water echinoderms break “Thorson’s Rule”. In *Reproduction, Larval Biology and Recruitment of the Deep-Sea Benthos*, ed. CM Young, KJ Eckelbarger, pp. 26–44. New York: Columbia Univ. Press
- Pearse JS, Lockhart SJ. 2004. Reproduction in cold water: paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep-Sea Res. II* 51:1533–49
- Pearse JS, McClintock JB, Bosch I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *Am. Zool.* 31:65–80
- Pechenik JA. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar. Ecol. Progr. Ser.* 177:269–97
- Poulin E, Feral J-P. 1996. Why are there so many species of brooding Antarctic echinoids. *Evolution* 50:820–30
- Rombough P. 2006. Developmental costs and the partitioning of metabolic energy. In *Comparative Developmental Physiology: Contributions, Tools, Trends*, ed. SJ Warburton, WW Burggren, B Pelster, CL Reiber, J Spicer. Oxford: Oxford Univ. Press
- Roughgarden J. 1989. The evolution of marine life cycles. In *Mathematical Evolutionary Theory*, ed. MW Feldman, pp. 270–300. Princeton: Princeton Univ. Press
- Salinas S, Munch SB. 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecol. Lett.* 15:159–63
- Schluter D, Price TD, Rowe L. 1991. Conflicting selection pressures and life history trade-offs. *Proc. R. Soc. Lond. B* 246:11–17

- Shanks AL, Grantham BA, Carr MH. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13:S159–69
- Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108:499–506
- Strathmann MF. 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. Seattle: Univ. Wash. Press
- Strathmann RR. 1974. The spread of sibling larvae of sedentary marine invertebrates. *Am. Nat.* 108:29–44
- Strathmann RR. 1985. Feeding and non-feeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Syst.* 16:339–61
- Strathmann RR. 1993. Hypotheses on the origin of marine larvae. *Annu. Rev. Ecol. Syst.* 24:89–117
- Thorson G. 1936. The larval development, growth and metabolism of arctic marine bottom invertebrates compared with those of other seas. *Medd. Grønland* 100:1–155
- Thorson G. 1946. Reproduction and larval development of Danish marine invertebrates with special reference to the planktonic larvae in the sound (Oresund). *Medd. Komm. Dan. Fisk. Havunder. Ser. Plankton* 4:1–523
- Thorson G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25:1–45
- Uthicke S, Schaffelke B, Byrne M. 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol. Monogr.* 79:3–24
- Van der Have TM, de Jong G. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. *J. Theor. Biol.* 183:329–40
- Vance RR. 1973. On reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107:339–52
- Von Bertanffy L. 1960. Principles and theory of growth. In *Fundamental Aspects of Normal and Malignant Growth*, ed. WW Nowinskii, pp. 137–259. Amsterdam: Elsevier
- Weersing K, Toonen RJ. 2009. Population genetics, larval dispersal, and connectivity in marine systems. *Mar. Ecol. Progr. Ser.* 393:1–12
- White JW, Botsford LW, Hastings A, Largier JL. 2010. Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. *Mar. Ecol. Progr. Ser.* 398:49–67
- Wilson NG. 2002. Egg masses of chromodorid nudibranchs (Mollusca: Gastropoda: Opisthobranchia). *Malacologia* 44:289–305
- Woods HA. 1999. Egg-mass size and cell size: effects of temperature on oxygen distribution. *Am. Zool.* 39:244–52
- Wray GA. 1995. Evolution of larvae and developmental modes. In *Ecology of Marine Invertebrate Larvae*, ed. LR McEdward, pp. 413–48. Boca Raton: CRC
- Young CM. 1990. Larval ecology of marine invertebrates: a sesquicentennial history. *Opbelia* 32:1–48



# Contents

Scaling Up in Ecology: Mechanistic Approaches <i>Mark Denny and Lisandro Benedetti-Cecchi</i> .....	1
Adaptive Genetic Variation on the Landscape: Methods and Cases <i>Sean D. Schoville, Aurélie Bonin, Olivier François, Stéphane Lobreaux, Christelle Melodelima, and Stéphanie Manel</i> .....	23
Endogenous Plant Cell Wall Digestion: A Key Mechanism in Insect Evolution <i>Nancy Calderón-Cortés, Mauricio Quesada, Hirofumi Watanabe, Horacio Cano-Camacho, and Ken Oyama</i> .....	45
New Insights into Pelagic Migrations: Implications for Ecology and Conservation <i>Daniel P. Costa, Greg A. Breed, and Patrick W. Robinson</i> .....	73
The Biogeography of Marine Invertebrate Life Histories <i>Dustin J. Marshall, Patrick J. Krug, Elena K. Kupriyanova, Maria Byrne, and Richard B. Emlet</i> .....	97
Mutation Load: The Fitness of Individuals in Populations Where Deleterious Alleles Are Abundant <i>Aneil F. Agrawal and Michael C. Whitlock</i> .....	115
From Animalcules to an Ecosystem: Application of Ecological Concepts to the Human Microbiome <i>Noah Fierer, Scott Ferrenberg, Gilberto E. Flores, Antonio González, Jordan Kueneman, Teresa Legg, Ryan C. Lynch, Daniel McDonald, Joseph R. Mihaljevic, Sean P. O'Neill, Matthew E. Rhodes, Se Jin Song, and William A. Walters</i> .....	137
Effects of Host Diversity on Infectious Disease <i>Richard S. Ostfeld and Felicia Keesing</i> .....	157
Coextinction and Persistence of Dependent Species in a Changing World <i>Robert K. Colwell, Robert R. Dunn, and Nyeema C. Harris</i> .....	183
Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change <i>Lauren B. Buckley and Joel G. Kingsolver</i> .....	205

Rethinking Community Assembly through the Lens of Coexistence Theory <i>J. HilleRisLambers, P.B. Adler, W.S. Harpole, J.M. Levine, and M.M. Mayfield</i> .....	227
The Role of Mountain Ranges in the Diversification of Birds <i>Jon Fjeldså, Rauri C.K. Bowie, and Carsten Rabbe</i> .....	249
Evolutionary Inferences from Phylogenies: A Review of Methods <i>Brian C. O'Meara</i> .....	267
A Guide to Sexual Selection Theory <i>Bram Kuijper, Ido Pen, and Franz J. Weissing</i> .....	287
Ecoenzymatic Stoichiometry and Ecological Theory <i>Robert L. Sinsabaugh and Jennifer J. Follstad Shab</i> .....	313
Origins of New Genes and Evolution of Their Novel Functions <i>Yun Ding, Qi Zhou, and Wen Wang</i> .....	345
Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts <i>Wim H. Van der Putten</i> .....	365
Inflammation: Mechanisms, Costs, and Natural Variation <i>Noah T. Ashley, Zachary M. Weil, and Randy J. Nelson</i> .....	385
New Pathways and Processes in the Global Nitrogen Cycle <i>Bo Thamdrup</i> .....	407
Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton Succession <i>Ulrich Sommer, Rita Adrian, Lisette De Senerpont Domis, James J. Elser, Ursula Gaedke, Bas Ibelings, Erik Jeppesen, Miquel Lüring, Juan Carlos Molinero, Wolf M. Mooij, Ellen van Donk, and Monika Winder</i> .....	429
Global Introductions of Crayfishes: Evaluating the Impact of Species Invasions on Ecosystem Services <i>David M. Lodge, Andrew Deines, Francesca Gherardi, Darren C.J. Yeo, Tracy Arcella, Ashley K. Baldridge, Matthew A. Barnes, W. Lindsay Chadderton, Jeffrey L. Feder, Crysta A. Gantz, Geoffrey W. Howard, Christopher L. Jerde, Brett W. Peters, Jody A. Peters, Lindsey W. Sargent, Cameron R. Turner, Marion E. Wittmann, and Yiwen Zeng</i> .....	449
<b>Indexes</b>	
Cumulative Index of Contributing Authors, Volumes 39–43 .....	473
Cumulative Index of Chapter Titles, Volumes 39–43 .....	477

## Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://ecolsys.annualreviews.org/errata.shtml>