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META-ANALYSIS

The biogeography of fertilization mode in the sea

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ABSTRACT

Aim Knowledge of the biogeography of life histories is central to understanding and predicting the impacts of global change on key functional traits that shape species distributions and transcend taxonomic boundaries. Whether species are internal or external fertilizers is a fundamental aspect of reproductive diversity in the sea, and has profound ecological and evolutionary consequences. However, geographic variation in this trait and the factors that potentially drive it (e.g. transitions in associated life-history traits, ecological conditions that favour one mode over the other or the evolutionary history of species) remain poorly characterized.

Location Oceans world-wide.

Methods We collated life-history data (modes of fertilization and development), geographic data and biophysical data (sea-surface temperatures and food availability) for 1532 marine species spanning 17 invertebrate phyla. We used standard and phylogenetic logistic regressions to evaluate latitudinal gradients in fertilization mode, plus their interactions with development (transitions from planktonic to aplanktonic development, or from feeding to non-feeding larvae) and taxonomy. We also explored the dependence of fertilization mode on biophysical variables to understand how ecology potentially contributes to geographic variation in this trait.

Results Fertilization mode often varies predictably with latitude, but the exact nature of this relationship depends on developmental mode and the phylum under consideration. Some commonalities were evident, however, with the likelihood of internal fertilization declining at higher latitudes for Annelida and Echinodermata with aplanktonic development, but increasing at higher latitudes for Cnidaria and Porifera with non-feeding, planktonic larvae. Synergistic effects of temperature and food availability may potentially shape some of these patterns.

Main conclusions There are latitudinal gradients in fertilization mode in the sea. The variation among phyla and developmental modes, however, is a complexity that is unexplained by existing theory. Combined effects of recent adaptation and deeper phylogenetic history have probably shaped this systematic variation in the reproductive ecology of marine organisms.

Keywords

Developmental mode, fertilization mode, functional biogeography, life histories, marine invertebrates, metazoans, reproductive strategies.

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INTRODUCTION

Renewed interest in trait-based approaches to explaining and modelling biodiversity has driven similar shifts in biogeography, expanding its strong historical focus on the species concept to the consideration of spatial patterns at higher organizational levels (Violle *et al.*, 2014). From this perspective, the biogeography of life histories is central to understanding and predicting the impacts of global change on ecosystem functioning, not only in terms of mapping species responses but also for mapping the

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responses of key functional traits that shape species distributions and transcend taxonomic boundaries (Green *et al.*, 2008; Violle *et al.*, 2014). To date, global patterns of biogeographic variation have been characterized for a number of life-history traits, including plant height and seed production (Moles *et al.*, 2009), body size (Blanckenhorn & Demont, 2004), offspring size (Marshall *et al.*, 2012) and mode of larval development (Thorson, 1936, 1946, 1950; Emlet, 1995; Mercier *et al.*, 2013). However, other important traits remain unexplored from a biogeographic perspective, leaving the presence, direction and magnitude of spatial patterns in their distributions entirely unknown.

Whether organisms reproduce by internal or external fertilization is one of the most fundamental aspects of reproductive diversity in aquatic taxa (e.g. invertebrates, fishes and amphibians) and has profound ecological and evolutionary consequences (Shine, 1978; Gross & Shine, 1981). By modulating the intensity of sexual selection and the benefits of parental care (Trivers, 1972; Williams, 1975), the mode of fertilization has major implications for the evolution of various life-history traits including developmental mode, adult body size, hermaphroditism and other sexual characteristics (Strathmann & Strathmann, 1982; Kerr *et al.*, 2011; Henshaw *et al.*, 2014). For example, males that shed gametes into the sea may evolve larger testes than males that copulate, possibly in response to the increased risk of sperm competition that often accompanies communal spawning (Stockley *et al.*, 1997). Similarly, fertilization mode may shape maternal investment by influencing a mother's capacity to predict the environmental conditions that her offspring are likely to face at critical stages of development (Einum & Fleming, 2002; Marshall & Keough, 2008). From a purely ecological perspective, the effects of fertilization mode on key drivers of population dynamics (including the direction and strength of density dependence; Levitan & Petersen, 1995) are manifold. Relative to species with internal fertilization, external fertilizers may be prone to greater recruitment variability (Thorson, 1950), greater sensitivity to environmental stressors (Byrne & Przeslawski, 2013) and greater vulnerability to Allee effects in the form of fertilization limitation as gametes become diluted at low population densities (Petersen & Levitan, 2001), to list just a few examples.

Despite the prime importance of fertilization mode, however, its distribution and underlying drivers in nature remain poorly resolved. In part, this knowledge gap may speak to the major legacies of classical biogeographers who regarded broad-scale biogeographic variation in this trait as both rare and unrelated to ecological conditions in the case of fishes (Turner, 1947) or largely absent in marine invertebrates (Thorson, 1946), even though variation in fertilization mode is now recognized as being common in both groups. Few studies have attempted to characterize the biogeography of fertilization mode in the subsequent decades, nor have any studies evaluated its macroecological correlates, despite ongoing speculation about the factors that might favour one mode over the other (e.g. Thorson, 1936; Menge, 1975; Chia, 1976; Jorgensen *et al.*, 2011) and the emergence of temperature and food availability, in particular, as likely candidates. For example, internal fertilization may be favoured when development rates are slower (as occurs for ectotherms at colder temperatures; O'Connor *et al.*, 2007; Jorgensen *et al.*, 2011), or when endogenous food for developing offspring is scarce (Menge, 1975; Wourms & Lombardi, 1992). Such predictions often conflate internal fertilization with the brooding of offspring, emphasizing their likely co-evolution (Wourms & Lombardi, 1992; but see Thorson, 1946). Again, however, we know of no studies that have formally evaluated the extent to which fertilization mode covaries with major transitions in other traits (e.g. from planktonic to aplanktonic development, or from feeding to non-feeding larvae) that serve related functions during early life history.

Marine invertebrates can offer crucial insights into the global distribution of fertilization mode. Not only do they account for a major proportion of the world's biodiversity and display remarkable variation in life histories (Strathmann, 1985, 1990), but the evolutionary history of extant animals suggests that the earliest metazoans were external fertilizers whose offspring developed, at least briefly, in the plankton before internal fertilization arose repeatedly in multiple lineages (Rouse & Fitzhugh, 1994; Wray, 1995; Hart *et al.*, 1997; Kerr *et al.*, 2011). Today, both internally and externally fertilizing species persist throughout most of the large invertebrate phyla and even co-occur within smaller clades (Strathmann & Strathmann, 1982; McHugh & Rouse, 1998), suggesting that fertilization mode can potentially evolve over relatively short time-scales and in ways that are not wholly dictated by phylogeny. Thus, the invertebrates provide an excellent opportunity for testing specific hypotheses about other phenotypic or ecological correlates of different fertilization modes in a formal statistical framework.

Here, drawing on a database of over 1500 marine species compiled from the literature, we describe the biogeography of fertilization mode across 140° of latitude and 17 invertebrate phyla using a logistic-regression framework that accounts for taxonomic non-independence among species (e.g. Ives & Garland, 2010). First, we explore latitudinal gradients in fertilization mode, and whether any such patterns differ among phyla or according to different modes of development. While we note that latitude *per se* might not influence such aspects of species reproductive biology, our focus on it here is motivated by its utility as a catch-all proxy for a range of as-yet unidentified geographic or ecological factors that possibly do. Next, given predictions that the ecological factors of temperature and food availability, specifically, act as agents of selection on fertilization mode (Menge, 1975; Jorgensen *et al.*, 2011), we test whether its distribution covaries with local sea-surface temperatures or phytoplankton abundance (the main source of endogenous food for invertebrate adults and larvae). Despite caveats arising from the inevitable sampling biases in compilations such as ours (see Methods), the present study is the most comprehensive evaluation of broad-scale biogeographic patterns in fertilization mode undertaken to date. As such, it represents an important step towards understanding patterns of global variation in this fundamental life-history trait. This may provide invaluable clues as to what circumstances might favour the evolution (or at least proliferation) of species with certain reproductive strategies, leading to their more effective conservation and management.

METHODS

Data collection and classification of life histories

We surveyed over 4000 studies (mostly primary literature, but occasionally unpublished theses) to assemble a database of life-history, geographic and biophysical data for 1532 marine species. These spanned 17 invertebrate phyla (see Appendix S1 in Supporting Information), but the vast majority (97%) belonged to the Annelida (various worms), Chordata (sea-squirts), Cnidaria (corals, jellyfish etc.), Echinodermata (sea-stars, sea-urchins etc.), Mollusca (bivalves, gastropods etc.) and Porifera (sponges). While most species were represented by one record, 91 species had multiple records (usually two, but four species had three) due mainly to synonymies decided since publication. In all cases, we ensured that each record comprised a unique observation of the species in question.

We recorded each species' fertilisation mode, classifying it as: (1) an external fertilizer if eggs were reported as fertilized outside the body of the female or (2) an internal fertilizer otherwise. Note that the latter classification does not distinguish between species with true copulation, those with pseudocopulation and those that shed sperm into the sea but retain eggs internally. Such information on the mode of sperm delivery was surprisingly unreported for many species (though many groups have converged on a single one, with copulation being largely absent among sessile, colonial taxa), due perhaps to a historical lack of appreciation for its ecological consequences or because it remains unresolved in many cases. Thus, this aspect of reproductive diversity remains an important avenue for future investigation but could not be formally incorporated into our scheme. Certain species still did not fit readily into this scheme: some tube-dwelling worms, for example, accomplish fertilization outside the female's body but within her tube, where embryos are brooded (Rouse & Fitzhugh, 1994). We classified such species, and analogous cases in other groups, as external fertilizers following experts in a particular group (e.g. Rouse & Pleijel, 2001, for the Annelida, which were the most challenging phylum in this regard). Importantly, our results were qualitatively unchanged when such ambiguous cases were excluded from analyses.

We also recorded each species' developmental mode, classifying it as: (1) aplanktonic (with no free-swimming larval stage), (2) planktonic feeding (with a swimming larval stage that must feed in the plankton to complete development), or (3) planktonic non-feeding (with a swimming larval stage that does not require exogenous food to complete development, or one that feeds only facultatively). Other schemes have been used to classify the diverse development of marine taxa (Krug, 2009), but ours is consistent with previous work (Marshall *et al.*, 2012) and encompasses both major dichotomies of marine larval ecology: planktonic versus aplanktonic larvae and feeding versus non-feeding larvae (a total of only three categories because no aplanktonic larvae feed exogenously).

Finally, we recorded the geographic coordinates of the collection site reported for each species in our database. To characterize the ecological attributes of each site, we accessed NASA's OceanColor Web (http://oceancolor.gsfc.nasa.gov/cms/) to extract sea-surface temperatures (from MODIS-Terra 9 km, 11 micron night) and chlorophyll *a* concentrations indicating phytoplankton abundances (from SeaWiFS 9 km) for these coordinates. Each site's data were averaged over 4 months (January, June, July and December) sampled from 1998 to 2008. Further details on our database, including data compilation and the relative merits of the life-history classifications used here, are available in Marshall *et al.* (2012).

Statistical analyses

Our overarching goal was to characterize the biogeography of fertilization mode in relation to latitude, developmental mode, taxonomy and ecology. The structure of our data, with some combinations of fertilization and development missing for certain phyla (due largely to the rarity of these combinations in nature), required a multistep approach to statistical analyses. All models were fitted using maximum likelihood in R 3.1 (R Core Team, 2014). We evaluated the overall significance of model effects using standard likelihood-ratio tests based on χ^2 distributions to compare the fits of full models and reduced models lacking the effect of interest, and evaluated the significance of regression coefficients (estimated once the appropriate model had been selected by the previous step) using Wald tests.

Standard logistic regressions

Our first step was to fit a standard logistic regression model (with fertilization mode as a binary response variable, developmental mode and phylum as categorical predictors and latitude as a continuous predictor) to all species. This model detected a significant three-way interaction between predictors ($\chi^2_{\text{latitude} \times \text{development} \times \text{phylum}} = 30.01$, d.f. = 10, $P < 0.01$), indicating that latitudinal gradients in fertilization mode differed among combinations of developmental mode and phylum. To confirm that the interaction was not simply an artefact of missing combinations of variables, we refitted the model to the only phyla for which variation in fertilization mode occurred for multiple developmental modes (i.e. the Annelida and Mollusca, accounting for 56% of species in our database; Fig. 1). This model gave a qualitatively similar result ($\chi^2_{\text{latitude} \times \text{development} \times \text{phylum}} = 6.32$, d.f. = 2, $P < 0.01$), prompting us to explore latitudinal gradients separately for each phylum and developmental mode with sufficient data. In addition to the Annelida and Mollusca, this included species of the Chordata, Cnidaria and Porifera with planktonic non-feeding development, and species of the Echinodermata with aplanktonic development. For these latter

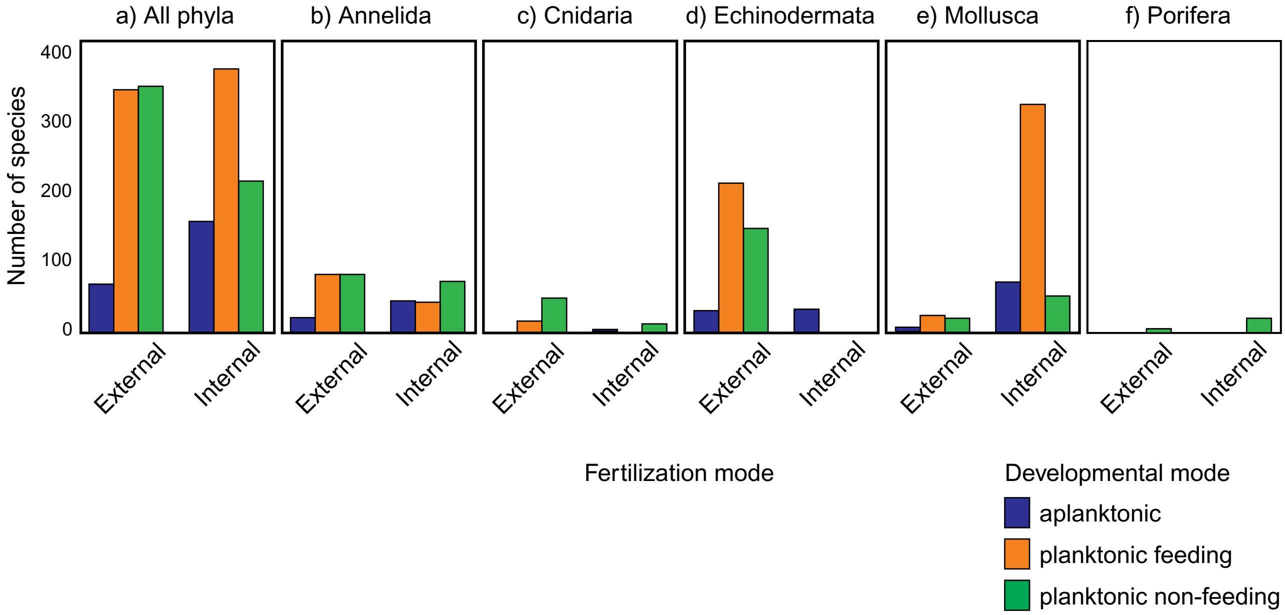

Figure 1 Summary of life-history traits (modes of fertilization and development): (a) pooled across phyla (totalling 1532 species) and (b)–(f) for each of five phyla that were analysed separately.

four phyla, species with other developmental modes lacked variation in fertilization mode (Fig. 1) and were omitted from subsequent analyses.

Phylogenetic logistic regressions

If related species tend to resemble each other, then this standard approach can potentially inflate type I error rates and incorrectly identify regression coefficients as significant (Ives & Garland, 2010). We therefore fitted a parallel set of models that accounted for such non-independence by estimating each set of regression coefficients given a specified tree of phylogenetic associations among species (Ives & Garland, 2010). In the absence of well-resolved molecular phylogenies for many of the species in our database, or even for key relationships near the base of the metazoan tree that are critical for inferring evolutionary relationships among phyla (Dunn *et al.*, 2014), we used taxonomy as a proxy. Briefly, we took phylum-to-species classifications for all records from the World Register of Marine Species (WoRMS), which provides expert-validated compromises between established systems and recent changes (WoRMS Editorial Board, 2015). We converted taxonomic variables to phylogenetic trees using phytools (Revell, 2012), then fitted trees in phylogenetic logistic regressions using phylolm (Ho & Ané, 2014; see also Ives & Garland, 2010). Before analysis, each tree was ultrametricized to make tips contemporaneous using Mesquite 3.03 (Maddison & Maddison, 2011) and scaled as a correlation matrix by setting its total height to 1.

We fitted a phylogenetic regression corresponding to each standard regression above, and include both sets of analyses here for completeness and to illustrate the impacts of phylogeny on our results. Since phylolm does not currently give omnibus tests of model effects (i.e. for the latitude × development interaction, which was of key interest here) or facilitate model-selection approaches for evaluating such effects, only Wald tests of phylogenetic regression coefficients are reported here. For comparison with a standard model fitted to all species, we fitted the analogous phylogenetic model using a combined tree with relationships among phyla left unresolved. While such a tree may not account for phylogenetic correlations due to deeper ancestry, phylum-specific models support all of our inferences about latitudinal gradients in fertilization mode.

Finally, to characterize the biogeography of fertilization mode in terms of the ecology of sites from which species were recorded, we fitted a phylogenetic regression to fertilization mode (as a binary response variable), sea-surface temperature, chlorophyll *a* concentration (as continuous predictors) and their interaction. Since latitude was strongly correlated with temperature ($r = -0.94$, $P < 0.01$) and, albeit to less extent, with chlorophyll ($r = 0.37$, $P < 0.01$), all three of these predictors could not be included in the same model without violating the assumption that such collinearity is absent. The model also included developmental mode, but treated as a binary, pseudo-continuous predictor classed only as feeding (coded as 0) or non-feeding (with aplanktonic and planktonic non-feeding developers pooled and coded as 1) to allow tests of its interactions with biophysical variables (Symonds & Blomberg, 2014). We refitted the model to all pairwise combinations of the three original categories of development to confirm that our results were qualitatively unchanged by this treatment. As with our final phylogenetic regression above, the model was fitted to data for all species using the same tree combined across phyla. Beyond accounting for taxonomic effects via this tree, we did not partition the model further by phylum because in many cases we considered we had too few our data to reliably support the added complexity of fitting surfaces (rather than lines, as in the case of latitudinal gradients above) at this level (Quinn & Keough, 2002).

Limitations of the database

As with any compilation of this kind, our data have limitations that are worth noting (see also Marshall *et al.*, 2012). English-language studies are over-represented, as are geographic regions that have been studied most intensively and habitats that are most accessible. For example, our records are biased toward coastal habitats of western Europe, North America, Australia, Scandinavia and certain parts of the tropics, whereas records from other tropical regions, Africa, much of South America, latitudes > 70° and from deeper waters that cover much of the planet, are under-represented in comparison. Different taxa have also received different levels of attention: for example, the genus *Conus* (cone shells) is exceptionally well-studied (due largely to the efforts of Kohn & Perron, 1994) and combines exclusively internal fertilization with a tropical distribution, as do sea slugs in the order Sacoglossa that are also prevalent in our database. This bias could potentially lead a certain fertilization mode being over-represented in certain regions, but should be substantially countered by our phylogenetic models. Finally, the geographic coordinates of each species' record may not be representative of its range as a whole, or of the biophysical conditions prevailing throughout. We cannot formally evaluate the severity of this problem without more detailed information on species distributions for our database; however, we speculate that it may make any trends observed here more conservative than not.

RESULTS

Overall, internal fertilization occurred in 69% of species with aplanktonic development, 52% of species with planktonic feeding development and 38% of species with planktonic non-feeding development (Fig. 1). Broken down by phylum, internal fertilization dominated all modes of development in the Mollusca and was common across all such modes in the Annelida. Otherwise, it was largely restricted to species of Echinodermata with aplanktonic development (although most species in this phylum were external fertilizers with planktonic development) and species of Chordata, Cnidaria or Porifera with planktonic non-feeding development.

Latitudinal gradients in fertilization mode

As noted above, preliminary modelling showed that latitudinal gradients in fertilization mode vary according to developmental mode and phylum. Setting the latter aside momentarily, a standard regression fitted to all species detected an interaction between latitude and developmental mode ($\chi^2_{\text{latitude} \times \text{development}} = 19.13$, d.f. = 2, $P < 0.01$), whereby species with aplanktonic development and those whose larvae feed planktonically are more likely to be internal fertilizers nearer the tropics before shifting toward predominantly external fertilization at higher latitudes, whereas species with planktonic, non-feeding larvae show no association between fertilization mode and latitude. Accounting for shared phylogeny, however, saw the latter gradient became significantly positive and the gradient for aplanktonic developers become non-significant (Fig. 2a, Table 1a).

With regard to individual phyla, standard regressions also found latitudinal gradients in fertilization to vary among developmental modes for the Annelida ($\chi^2_{\text{latitude} \times \text{development}} = 9.75$, d.f. = 2, $P < 0.01$), with internal fertilization predicted to decline from the tropics poleward for aplanktonic species and species with non-feeding larvae, but species with feeding larvae showing an opposing but non-significant trend (Fig. 2b, Table 1b). No such interaction was evident for the Mollusca ($\chi^2_{\text{latitude} \times \text{development}} = 1.05$, d.f. = 2, $P = 0.59$): regardless of developmental mode, the odds of internal fertilization in this group are overwhelmingly high nearer the tropics but decrease steadily with increasing latitude ($\chi^2_{\text{latitude}} = 34.08$, d.f. = 1, $P < 0.01$; Fig. 2e, Table 1e). Again, accounting for shared phylogeny modified these patterns, rendering only the negative gradient for aplanktonic developers significant for the Annelida and eliminating latitudinal effects entirely for the Mollusca.

Standard and phylogenetic regressions were remarkably consistent for the remaining phyla in which a single developmental mode was analysed. Latitudinal gradients in fertilization were significantly positive (with internal fertilization increasingly likely at higher latitudes) for both the Cnidaria and Porifera with planktonic non-feeding larvae (Fig. 2c, f, Table 1c, f), but significantly negative (with internal fertilization increasingly likely at lower latitudes) for the Echinodermata with aplanktonic development. No patterns were evident for the Chordata (results not presented here).

Covariation of fertilization mode with biophysical variables

Our phylogenetic regression fitted to all species detected interactive effects of sea-surface temperature and phytoplankton abundance (measured by chlorophyll *a* concentration) on fertilization mode. No effects involving developmental mode were significant (Table 2). Plotting the model's predicted values against biophysical variables (Fig. 3) shows that internal fertilization is expected to dominate in cooler waters where phytoplankton is abundant (i.e. those combining mean surface temperatures below *c.* 16°C with chlorophyll *a* concentrations above *c.* 8 g m^{-3}; Fig. 3). However, external fertilization becomes increasingly likely as phytoplankton declines or sea temperature rises, to the point of being favoured in the coldest, most oligotrophic waters or the warmest food-rich ones (Fig. 3).

DISCUSSION

While biogeographic variation has traditionally been studied in terms of species distributions, attention has increasingly turned

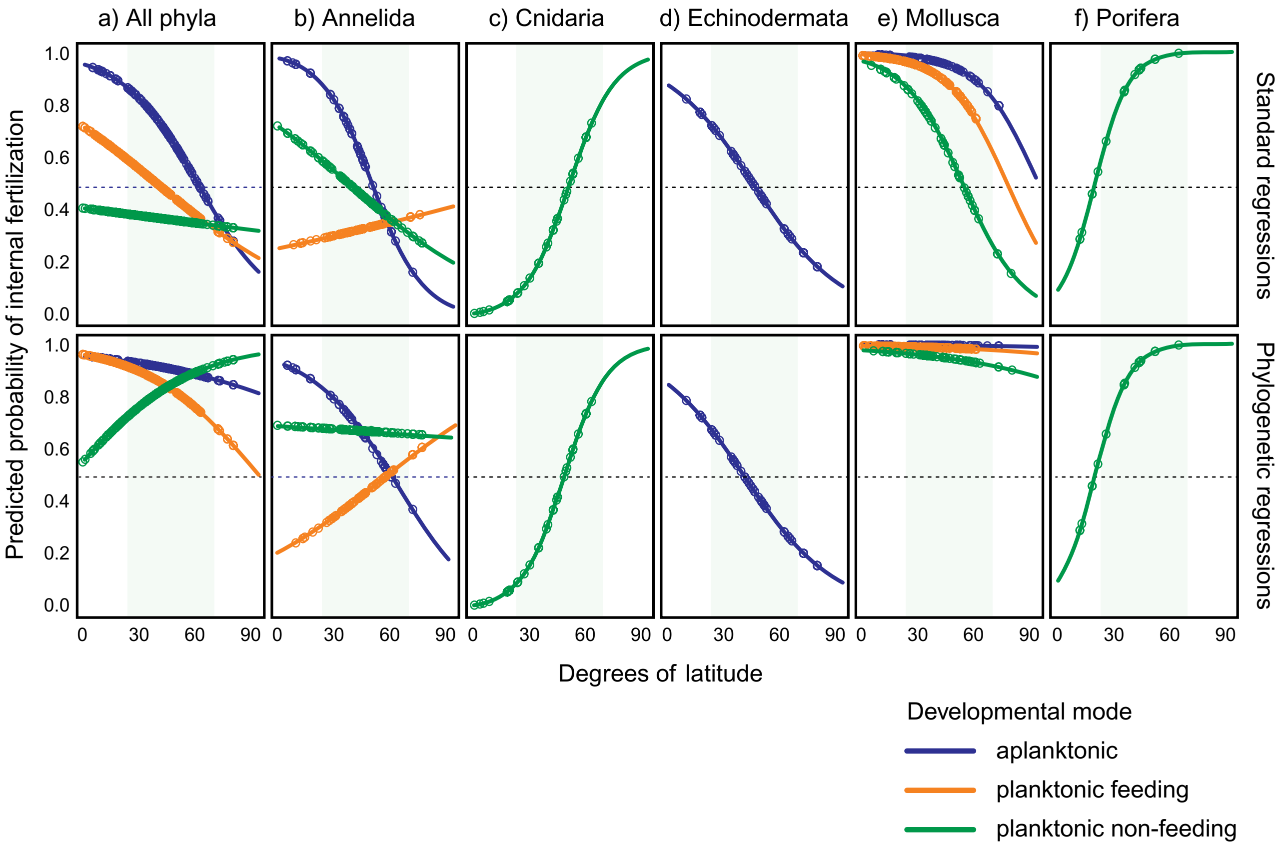

Figure 2 Latitudinal gradients in fertilization mode, fitted for each developmental mode with sufficient data: (a) pooled across phyla and (b)–(f) estimated for each of five phyla analysed separately. Gradients are lines of best fit estimated by logistic regression (species fitted values are superimposed on lines to show distributions of data across latitudes). Upper panels show standard regressions uncorrected for species associations, while lower panels show phylogenetic regressions that account for those associations (see text for details). To aid interpretation, temperate latitudes are shaded in each panel and a dashed line marks where both fertilization modes are predicted to be equally likely.

to the distributions of functional traits expressed by those species, which may unify them in ways that phylogeny does not (Green *et al.*, 2008; Violle *et al.*, 2014). This shift in focus is particularly welcome for marine systems, where much of the remarkable diversity of life histories still awaits formal synthesis and explanation, and their apparent decoupling from phylogeny is one of the few generalizations currently available (e.g. Hart *et al.*, 1997; Krug, 2009; Marshall *et al.*, 2012). Our results provide the first empirical evidence of latitudinal gradients in the global distribution of fertilization mode in the sea, though these gradients vary in strength and direction according to developmental mode as well as the phylum under consideration. Replacing latitude with two of its key biophysical correlates in our models, moreover, suggests that latitudinal variation in fertilization mode may be mediated by variation in sea temperature and planktonic food availability, which had synergistic effects on the predicted distributions of internal and external fertilizers. Some of our results have been anticipated by theory, while other patterns revealed here were surprising.

There is little theory to explain variation in fertilization mode *per se* (Henshaw *et al.*, 2014) and none, to our knowledge, explores its association with latitude. Based on the predicted effects of temperature on developmental rates (O'Connor *et al.*, 2007), we expected internal fertilization to be more prevalent at higher latitudes than at lower ones because cooler climates prolong development, thereby prolonging the exposure of free-swimming larvae to various sources of mortality (advection, predation and starvation) in the plankton (Morgan, 1995). Consequently, selection may act to reduce larval duration in colder waters, favouring life-histories that afford offspring the protection of the mother's body for as long as possible, and presumably inclusive of fertilization itself. Consistent with this expectation, Marshall *et al.* (2012) reported a higher incidence of aplanktonic development at higher latitudes than in the tropics for a subset of species in our database. Here, however, it proved to be an overly simplistic explanation for latitudinal gradients in fertilization mode. Species with non-feeding larvae showed the expected pattern, driven mainly by the Cnidaria and Porifera, as did species of Annelida with feeding larvae. Other groups showed little pattern at all once phylogeny was taken into account (e.g. the Mollusca) or ran contrary to expectation in the case of aplanktonically developing species of Annelida and

Table 1 Standard and phylogenetic logistic regressions testing latitudinal gradients in fertilization mode: (a) pooled across phyla and (b)–(f) for each of five phyla analysed separately. Regression coefficients are estimated by developmental mode (aplanktonic, planktonic feeding or planktonic non-feeding). Intercepts have been omitted for brevity. *P*-values use Wald-type *z*-statistics based on division of coefficients by their standard errors.

	Standard regressions		Phylogenetic regressions	
	Latitudinal gradient (SE)	*P*-value	Latitudinal gradient (SE)	*P*-value
(a) All phyla				
Aplanktonic	−0.05 (0.01)	< 0.01	−0.02 (0.01)	0.13
Planktonic feeding	−0.02 (0.00)	< 0.01	−0.03 (0.01)	< 0.01
Planktonic non-feeding	0.00 (0.01)	0.48	0.03 (0.01)	< 0.01
(b) Annelida				
Aplanktonic	−0.08 (0.02)	< 0.01	−0.04 (0.02)	0.02
Planktonic feeding	0.01 (0.01)	0.59	0.03 (0.01)	0.09
Planktonic non-feeding	−0.03 (0.01)	0.03	0.00 (0.01)	0.96
(c) Cnidaria				
Planktonic non-feeding	0.09 (0.03)	< 0.01	0.09 (0.04)	0.01
(d) Echinodermata				
Aplanktonic	−0.04 (0.02)	< 0.01	−0.04 (0.02)	< 0.01
(e) Mollusca				
Aplanktonic	−0.07 (0.02)	< 0.01	−0.02 (0.03)	0.48
Planktonic feeding				
Planktonic non-feeding				
(f) Porifera				
Planktonic non-feeding	0.12 (0.05)	0.03	0.11 (0.05)	0.03

Table 2 A phylogenetic logistic regression testing the response of fertilization mode to interacting effects of sea-surface temperature, food availability in terms of phytoplankton abundance (measured by chlorophyll *a* concentration) and developmental mode (feeding or non-feeding; see text for details). *P*-values use Wald-type *z*-statistics based on division of coefficients by their standard errors.

	Regression coefficient (SE)	*P*-value
(Intercept)	−1.35 (0.55)	0.01
Sea-surface temperature	0.05 (0.01)	< 0.01
Chlorophyll *a* concentration	0.35 (0.10)	< 0.01
Developmental mode	0.57 (0.34)	0.09
Temperature × chlorophyll *a*	−0.02 (0.01)	< 0.01
Temperature × developmental mode	−0.02 (0.02)	0.17
Chlorophyll *a* × developmental mode	−0.21 (0.12)	0.09
Temperature × chlorophyll *a* × developmental mode	0.01 (0.01)	0.07

Echinodermata, for which internal fertilization is predicted to decline at higher latitudes to the point of being the rarer fertilization mode in cooler waters for the latter phylum. We cannot currently explain this result. Admittedly, our expectation relied on the assumption that brooding of offspring is effectively a proxy for internal fertilization, given the functional overlap between them (Gross & Shine, 1981). Clearly, however, their biogeographic distributions do not fully match, arguing that the ecological and evolutionary consequences of fertilization mode are at least partly independent of development, or interact with it in more complex ways than anticipated, and warrant further investigation.

Nevertheless, our study does support a link between fertilization and developmental modes, albeit a highly context-dependent one. This insight alone may help resolve the long-standing debate as to whether life histories in the sea show any such pattern. A key hypothesis for the evolution of parental investment emphasizes the degree of association between parent and offspring (Williams, 1975), which is higher for females in the case of internal fertilization and is thought to explain its coincidence with brooding and viviparity in teleost fishes (Gross & Shine, 1981). However, Thorson (1946, p. 429) declared that ‘no connection seems to exist between the mode of oviposition and the mode of development in marine invertebrates’, and subsequent work (e.g. Strathmann, 1985; McHugh & Rouse, 1998; Kupiyanova *et al.*, 2001) has variously upheld and contradicted his position. Our results go some way toward explaining why. Throughout the taxonomic range considered here, species with aplanktonic larvae are typically internal fertilizers (Fig. 1), echoing the case in teleosts (Gross & Shine, 1981). This pattern is particularly extreme and holds globally (but does so irrespective of development) in the Mollusca – whose prevalence in our database probably drove a similar outcome in our combined analysis of all phyla (Fig. 2a), obscuring the latitudinal effects on fertilization that accompany aplanktonic development in the Annelida and Echinodermata alone. For the latter, moreover, internal fertilization is absent among species with planktonic larvae, lending further weight to the idea that (for some taxa at least) transitions from external to internal fertilization have coincided with transitions from planktonic to aplanktonic development.

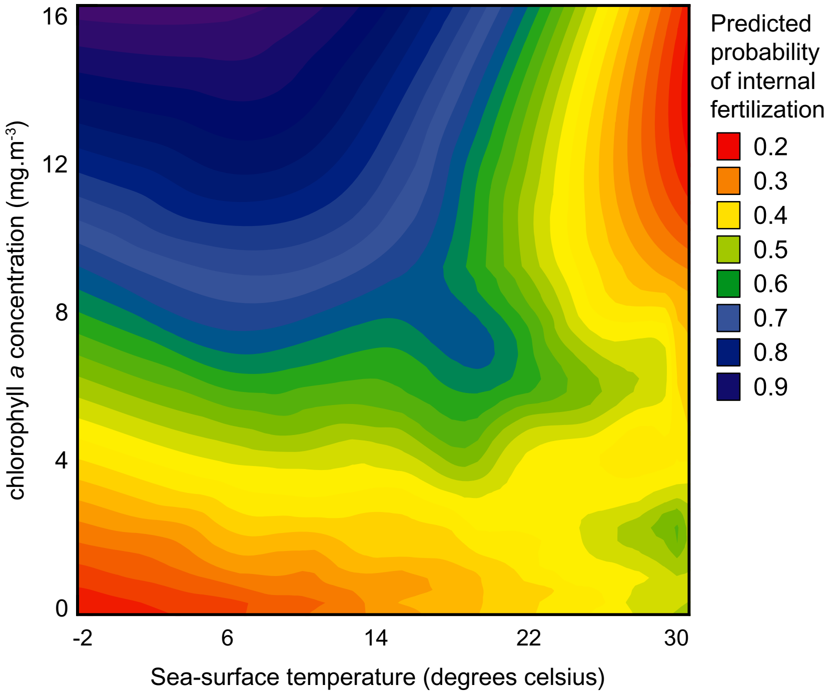

Figure 3 The relationship between fertilization mode, sea-surface temperature and food availability in terms of phytoplankton abundance (measured by chlorophyll *a* concentration). The figure shows the surface of best fit estimated by phylogenetic logistic regression (see Table 2), with cooler colours indicating higher probabilities of internal fertilization.

For other taxa, however, it depends where on Earth you look: the interplay of latitude with fertilization and development means that the hypothesis of Williams (1975) holds for some phyla in some regions (e.g. internal fertilization is predicted for Annelida with aplanktonic larvae in the tropics) but fails elsewhere (e.g. such fertilization is also predicted for tropical Mollusca with planktonic larvae). Thus, while our results provide new evidence of covariation between these major life-history traits across a range of invertebrate phyla, we lack sufficient insight into the underlying mechanisms to understand why the exact form of their association varies regionally and taxonomically.

A closer look at the biophysical correlates of latitude leads to the suggestion that ecology may play a key role in driving at least some of the above patterns. Temperature and food availability have long been proposed as ecological factors likely to shape adaptive variation in fertilization mode – for example by favouring brooding in colder waters that prolong development (as noted above) or in less productive waters that offer limited nutrition for feeding larvae (Menge, 1975; Wourms & Lombardi, 1992; Jorgensen *et al.*, 2011). Here, we found these ecological factors to have a synergistic association with the global distribution of fertilization mode that is more nuanced than anticipated and offers only equivocal support for such proposals. For example, when food is relatively abundant, the relationship between temperature and fertilization mode is much as predicted, with predominantly internal fertilization in colder waters giving way to predominantly external fertilization in warmer ones. Indeed, this remains the case throughout the very warmest waters regardless of their productivity (which may play a greater role in mediating the likelihood of feeding versus non-feeding development, though Marshall *et al.*, 2012, detected no such effect). Harder to explain, however, is the relationship between productivity and fertilization mode in cooler waters, since its direction (i.e. with higher productivity favouring internal fertilization) goes against the notion that the global distribution of external fertilizers is driven by the nutritional requirements of planktonic larvae. Rather, it might be that the energetic costs of brooding paid by mothers, and the potential interaction of these costs with food availability, do more to explain the low likelihood of internal fertilization in oligotrophic waters predicted by our results. The prevalence and magnitude of such costs remains an open question.

As with any other trait, however, the present biogeography of fertilization mode is likely to be an admixture of recent adaptive variation and deeper ancestry (Freckleton & Jetz, 2009; Violle *et al.*, 2014). Our evaluation of ancestral effects here was limited to using taxonomy as a proxy for phylogenetic associations within phyla, and makes no attempt to account for deeper relationships among phyla that are currently unresolved (Dunn *et al.*, 2014). These limitations aside, our discovery that latitudinal gradients in fertilization mode differ taxonomically implies that the evolutionary history of species has left a lasting imprint on biogeographic variation in this trait, with varying consequences for its ongoing malleability. For example, the convergence on similar distributions of fertilization mode by phylogenetically distant groups (e.g. the Cnidaria and Porifera; Fig. 2c, f) might mean that their members have adapted to similar geographic clines in selection pressures. Conversely, members of other groups for which a single fertilization mode is largely conserved globally could share phylogenetic constraints that have hindered evolutionary divergence in this trait, or else hindered the success of divergent lineages (Losos, 2011). Several taxa in our database support this idea. Internal fertilization has either had limited opportunity to arise or failed to become established in Echinodermata with planktonic development, given its absence among the many species that we sampled from this group. Similarly, shared ancestry explains much of the variation in fertilization mode among the Mollusca, with the contrast between upper and lower panels in Fig. 2(e) suggesting that external fertilization has arisen relatively rarely in the phylum and done so relatively deep in its evolutionary history, or at least prior to the diversification of developmental modes. Such speculation, of course, assumes that our database accurately reflects at least the relative abundances of alternative reproductive strategies across taxa, and that transitions in fertilization mode are irreversible. However, the latter assumption fails to hold for the extraordinarily labile Annelida at least (Rouse & Fitzhugh, 1994; McHugh & Rouse, 1998), emphasizing that fundamental questions about the order, direction and stability of major transitions in metazoan life histories remain unanswered.

In summary, our study adds to recent progress in characterizing global patterns in marine life histories (Marshall *et al.*, 2012; Mercier *et al.*, 2013). Evidence of latitudinal gradients in fertilization mode, plus evidence of their interplay with ecology, taxonomy and other major life-history traits, not only sheds new light on outstanding questions about the evolution of life histories in the sea but highlights a number of areas worthy of research or re-evaluation: To what extent do modes of fertilization and development co-evolve, given that their respective geographic distributions show their association to be more context-dependent than is often appreciated? What are the relative contributions of phylogeny and recent adaptation to global variation in reproductive strategies? Do ecological factors such as temperature and food availability still exert selection on reproductive strategies, and if so how are marine life histories (including those of fishes with similar reproductive diversity) likely to respond to forecast global change, and how should they be managed accordingly? No doubt, some of these questions are best addressed in a comparative framework (e.g. by mapping major transitions in life-history traits onto robust phylogenies), while others may benefit from experimental (e.g. quantitative genetic) approaches that can elucidate how various microevolutionary forces shape the kinds of broader-scale patterns that we have identified here.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Species records used in this study, organized by phylum, fertilization mode and developmental mode.

BIOSKETCHES

Keyne Monro is an evolutionary ecologist who works on benthic marine invertebrates and seaweeds. She studies broad questions relating to life-history evolution, how variation in life histories manifests within and among species and how such variation is shaped by genetic and environmental influences.

Dustin Marshall is an evolutionary ecologist with a focus on marine invertebrate life histories. Dustin seeks to understand variation in marine life histories at both a macroevolutionary scale using biogeographical approaches and at a microevolutionary scale using the techniques of quantitative genetics.

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