Fertilization Mode Covaries with Body Size

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ABSTRACT: The evolution of internal fertilization has occurred repeatedly and independently across the tree of life. As it has evolved, internal fertilization has reshaped sexual selection and the covariances among sexual traits, such as testes size, and gamete traits. But it is unclear whether fertilization mode also shows evolutionary associations with traits other than primary sex traits. Theory predicts that fertilization mode and body size should covary, but formal tests with phylogenetic control are lacking. We used a phylogenetically controlled approach to test the covariance between fertilization mode and adult body size (while accounting for latitude, offspring size, and offspring developmental mode) among 1,232 species of marine invertebrates from three phyla. Within all phyla, external fertilizers are consistently larger than internal fertilizers: the consequences of fertilization mode extend to traits that are only indirectly related to reproduction. We suspect that other traits may also coevolve with fertilization mode in ways that remain unexplored.

Keywords: fertilization mode, body size, life history, macroevolution.

Introduction

The evolution of internal fertilization—from releasing gametes into the external environment to transferring them internally—was a critical biological innovation with profound consequences for selection (Parker 1970, 1984; Williams 1975; Shine 1978; Gross and Shine 1981; Parker and Pizzari 2010). From snails to fishes to frogs, internal fertilization has evolved frequently and independently across the tree of life, with both ecological and evolutionary consequences (Parker 1970; Franzén 1977; Duellman and Trueb 1986; Wootton and Smith 2014; Kahrl et al. 2021). Fertilization mode influences population dynamics: relative to internal fertilizers, external fertilizers may experience more variable recruitment (Thorson 1950; Strathmann and Strathmann 1982) and be more prone to Allee effects (Levitan et al. 1992; Levitan and Petersen 1995; Levitan 1998). Fertilization mode also modifies the intensity of

both natural selection and sexual selection: internal fertilizers face fierce competition to copulate, and ejaculates from different males compete to win fertilizations within the female reproductive tract (Parker 1970, 1984). Meanwhile, external fertilizers face the challenge of achieving fertilization success at all, which can be limited by access to too few (sperm limitation) or too many (polyspermy) sperm (Vogel et al. 1982; Styan 1998; Styan and Butler 2000; Millar and Anderson 2003; Bode and Marshall 2007).

Perhaps unsurprisingly, different fertilization modes select for different suites of reproductive traits. In internal fertilizers, males tend to have smaller ejaculates, larger (perhaps more competitive) sperm, and relatively small testes, while external fertilizers show the opposite patterns (Franzén 1956, 1970, 1977; Stockley et al. 1996, 1997; Kahrl et al. 2021). Selection on egg size also differs between internal fertilizers and external fertilizers: in internal fertilizers, fertilization success is relatively ensured once mating has occurred, but in external fertilizers, fertilization success is fraught and most eggs can go unfertilized (e.g., Marshall 2002). The covariance between fertilization mode and reproductive traits is clear. Whether fertilization mode covaries with traits that are not directly related to reproduction remains unknown, yet there are clear expectations that fertilization mode should alter selection on such traits.

Fertilization mode should covary with body size. External fertilizers should be larger than internal fertilizers, a prediction that emerges independently from different models with different foci, specifically models of resource availability/energy budgets (hence, body size; Williams et al. 2005) and models of sperm limitation (Henshaw et al. 2014). Henshaw et al. (2014) suggest that sperm limitation severely reduces fertilization success in small external fertilizers (because sperm quickly dilute when released into the water column), such that selection should favor larger adult body sizes in external fertilizers and smaller body sizes in internal fertilizers. This theory had informal antecedents that made

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similar predictions (Strathmann and Strathmann 1982). Testing these predictions is not straightforward however, because fertilization mode is often confounded with other life history traits or phylogeny.

Fishes and amphibians show both internal fertilization and external fertilization across species, so assessing whether fertilization mode covaries with body size in these groups has intuitive appeal. However, in fishes, most species that are external fertilizers are also oviparous (egg laying), and many species that are internal fertilizers are also viviparous (live bearing; Mank et al. 2005; Wootton and Smith 2014; but see Abe and Munehara 2009; Muñoz 2010). We have good reason to expect reproductive mode to also shape body size independently of fertilization mode (Day and Taylor 1997, 2000), so getting a "clean" test of fertilization mode effects on body size is difficult in fishes. Fertilization mode also varies in amphibians, but the transition from external to internal fertilization occurred deep in the phylogeny such that nearly all anurans (frogs and toads) are external fertilizers and most urodeles (salamanders and newts) and all caecilians (limbless amphibians) are internal fertilizers (Halliday and Verrell 1984; Duellman and Trueb 1986; Charney et al. 2014). As such, there might be a covariance between body size and fertilization mode in amphibians, but interpreting such a covariance would be challenging: if newts are smaller than frogs, is it because newts are internal fertilizers specifically or simply because they are newts?

Marine invertebrates provide clearer tests of the covariance between body size and fertilization mode. In some phyla, around half of all species are internal fertilizers, and fertilization mode has evolved independently of reproductive mode many times, even among congeners (Monro and Marshall 2015; Kahrl et al. 2021). Indeed, a number of studies explore how fertilization mode and various other traits covary with each other in various marine invertebrate groups (Strathmann and Strathmann 1982; Hendler and Littman 1986; Rouse and Fitzhugh 1994; Hart et al. 1997; Kupriyanova et al. 2001; McFadden et al. 2001), but comprehensive, phylogenetically controlled tests across a wide range of clades are lacking.

Here, we use a phylogenetically controlled approach to test the theoretical predictions for how fertilization mode should covary with body size in >1,200 species of marine invertebrates, spanning three phyla (annelids, echinoderms, and mollusks). Because body size sometimes covaries with offspring size (Neuheimer et al. 2015; Olsson et al. 2016; Rollinson and Rowe 2016; Rollinson et al. 2019) and latitude (Bergmann 1847; Watt et al. 2010; Rollinson and Rowe 2018; Campbell et al. 2021), we also included these factors in our analyses.

Methods

Data Collection and Classification of Life History Traits

We compiled data for adult size, fertilization mode, and latitude for 1,232 species of marine annelids (330 spp.), echinoderms (427 spp.), and mollusks (475 spp.), and for a subset of the species for which it was available, we compiled additional data for offspring size (993 spp. total: 239 annelids, 371 echinoderms, and 383 mollusks). Because fertilization mode is sometimes associated with offspring developmental mode in marine invertebrates (Strathmann and Strathmann 1982; Rouse and Fitzhugh 1994; Hart et al. 1997; Kupriyanova et al. 2001; Monro and Marshall 2015), we also recorded each species' developmental mode (aplanktonic, planktonic nonfeeding, or planktonic feeding; sensu Marshall et al. 2012) to test the relative influence of these two traits on body size. The species in our dataset came from previously published meta-analyses on various marine invertebrate life history traits (Marshall et al. 2012; Monro and Marshall 2015), supplemented with additional data for adult size from the literature.

Unfortunately, we could not follow a formal preferred reporting items for systematic reviews and meta-analyses (PRISMA) approach (Page et al. 2021) because data for adult size, life history, and latitude are rarely reported in a single source. Instead, once we determined the fertilization mode of the species, we then searched for more information on the adult size, latitude, developmental mode, and offspring size for that species. Information was collected from studies from Google Scholar (https://scholar.google.com/) based on the following search terms: "[*Genus species*]" together with the terms "develop*", "development* mode", "weight", "size", "adult size", "mass", "adult mass", "egg*", "egg size", "egg diameter", "offspring size", or "latitud*". Within those selected articles, we also explored relevant citations to identify as many studies as possible.

We collected data for adult size (i.e., grams total wet weight of sexually mature individuals), offspring size (i.e., egg diameter [μm]), and latitudinal coordinates for collection sites from the literature, supplemented with information from online databases (e.g., World Register of Marine Species: http://www.marinespecies.org/; SeaLifeBase: https://www.sealifebase.ca/). When adult sizes were reported as dry masses or lengths, we converted to wet weight based on conversion factors from Brey et al. (2010) and Robinson et al. (2010). Note that our classification of adult size does not differentiate between males and females—such information was unreported for many species (particularly external fertilizers) and therefore could not be formally tested here. Whether the covariance between body size and fertilization mode differs between males and females is an important avenue for future research, and we encourage empiricists to

report the sex of their study organisms when measuring body size.

We classified fertilization mode as external if eggs were reported as being fertilized outside the body of the female and as internal otherwise. Similar to Monro and Marshall (2015), our classification scheme relied on the expertise of empiricists who originally classified the fertilization mode of each species (e.g., Strathmann 1987 for all three phyla; Rouse and Pleijel 2006 for annelids). Under this classification, sperm casters (i.e., species that release sperm into the sea but retain eggs internally) as well as species with true copulation or pseudocopulation were considered internal fertilizers. Unfortunately, this level of detail is unreported or unknown for many of the internal fertilizers in our dataset. However, for a subset of our species for which this information was known (73 spp. total: 28 annelids, 3 echinoderms, and 42 mollusks; table S6), we were able to compare body sizes between copulators and sperm casters (see the supplemental PDF for further details). Notably, body size does not differ between these two groups (table S7).

Statistical Analyses

We characterized the covariance between adult size and fertilization mode (fig. 1) while accounting for the effect of latitude, offspring size, or developmental mode in three separate models. For the models that included offspring size or latitude, we tested patterns in body size both within phyla and among phyla. For the model that included developmental mode, we could not test patterns within phyla because some combinations of fertilization mode and developmental mode are rare in nature and absent in our dataset (e.g., there are no echinoderms with both internal fertilization and planktonic feeding development in our dataset; table 1).

We analyzed our data with phylogenetically controlled models to account for the influence of species' shared evolutionary history on patterns in body size (Felsenstein 1985). Specifically, our models assessed whether there is an association between body size and fertilization mode, along with our other traits of interest, while incorporating the covariation among species due to phylogenetic relatedness into the models' error structure (Harvey and Pagel 1991; Rohlf 2001; Ives 2018). Our three models included natural-log-transformed body mass as the continuous response variable and fertilization mode as a categorical predictor, with developmental mode (categorical), latitude (continuous), or natural-log-transformed offspring size (continuous) as additional predictors.

We fitted phylogenetic generalized least squares (PGLS) regressions (Grafen 1989; Martins and Hansen 1997; Garland and Ives 2000; Smaers and Rohlf 2016) with the gls function in the package ape (ver. 5.6-2;
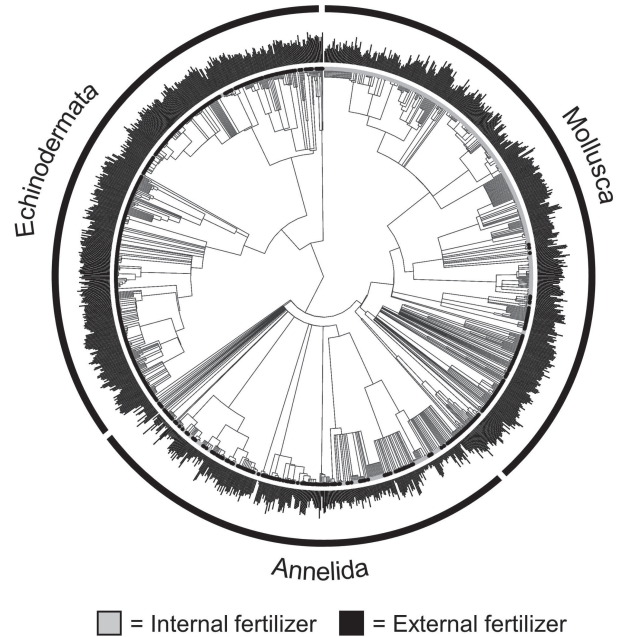

Figure 1: Adult body mass (black bars; estimated as natural-log-transformed wet weight [g]) mapped to the phylogeny of species in our dataset. Colored circles at the tips of the tree indicate whether the species is an internal fertilizer (gray) or external fertilizer (black). Data were available for three phyla: Annelida ($n = 330$), Echinodermata ($n = 427$), and Mollusca ($n = 475$).

Paradis and Schliep 2019). We first evaluated the significance of model predictors using F-tests, reducing models in which interactions were not significant ($P > .05$). Next, we evaluated the significance of regression coefficients (once the appropriate model had been selected from the previous step) using Wald tests.

We extracted our phylogeny from the Open Tree of Life (Hinchliff et al. 2015) with the package rotl (ver. 3.0.14; Michonneau et al. 2016) and constructed phylogenetic trees with the package phytools (ver. 1.2-0; Revell 2012). Branch lengths from the Open Tree of Life are not time calibrated. Therefore, we used the function congruify.phylo (Eastman et al. 2013) with the PATHd8 scaling method (Britton et al. 2007) in the package geiger (ver. 2.0.10; Harmon et al. 2008; Pennell et al. 2014) to time calibrate our tree according to time data from the TimeTree of Life (Kumar et al. 2022). This function maps known species' divergence times from a reference tree (time calibrated) to a target tree (uncalibrated) sampled from the same lineage. We then randomly resolved all polytomies in our time-calibrated tree with the function multi2di (package ape).

We tested the fit of Brownian motion (BM; corBrownian), Pagel's λ (PL; corPagel), and Ornstein-Uhlenbeck (OU; corMartins) models of character evolution for body size (package ape). First, we compared PL and OU models with

Table 1: Species records used in this study, organized by phylum and life history traits

Phylum, fertilization mode	Offspring size ($n = 993$)	Developmental mode ($n = 1,232$)		
		Aplanktonic	Planktonic nonfeeding	Planktonic feeding
Annelida:				
Internal	104	25	102	31
External	135	4	87	81
Echinodermata:				
Internal	31	30	6	…
External	340	28	147	216
Mollusca:				
Internal	309	71	48	232
External	74	1	48	75

BM models with likelihood ratio tests: for all models, PL and OU models fit the data better than BM models (table S1). Next, we compared the PL model with the OU model using Akaike information criterion (AIC; Akaike 1978; Quinn and Keough 2002). In all cases, the PL model was a better fit than the OU model according to lowest AIC values and ΔAIC > 2 (table S1), so we used models fitted with PL correlation structure for all analyses.

We ran an additional model to compare body sizes between congeners that differ in their fertilization mode within each phylum (table S4). Unlike the PGLS models mentioned above, we used a linear mixed effects model (lmer function in package lme4 ver. 1.1–31; Bates et al. 2015) with natural-log-transformed body mass as the response variable, fertilization mode as a fixed categorical predictor, and species nested within genus as a random effect. We evaluated the overall significance of fertilization mode with analysis of deviance tests based on χ^2 distributions with the package car (ver. 3.1-1; Fox and Weisberg 2019) and the significance of regression coefficients based on t-tests with Satterthwaite's (1941, 1946) method.

We completed all analyses in RStudio (ver. 4.2.2; RStudio Team 2022). Figures were created using the packages ggplot2 (ver. 3.3.5; Wickham 2016), ggtree (ver. 3.6.2; Yu et al. 2017; Yu 2022), and ggtreeExtra (ver. 1.8.1; Xu et al. 2021).

Results

Fertilization Mode and Latitude versus Body Size

In all three phyla, external fertilizers are larger than internal fertilizers (fertilization: $F_{1,1,229} = 98.13$, $P < .01$; fig. 2). These patterns are most pronounced in annelids, followed by echinoderms, then mollusks, where external fertilizers are 12.2, 5.8, and 5.4 times larger than internal

fertilizers, respectively (tables S2, S3). Latitude does not covary with body size at all (table S2).

Our findings suggest that two congeners that are identical in their life histories (e.g., offspring size, developmental mode) but differ in their fertilization mode can have vastly different body sizes. In our dataset, there are 25 genera that contain both internally fertilizing species and externally fertilizing species (table S4). Within these genera, external fertilizers are 3.7 and 5.5 times larger than internal fertilizers
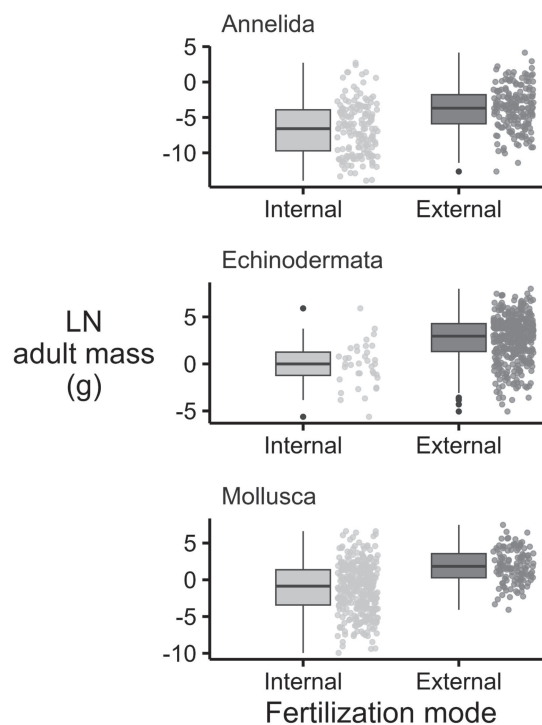

Figure 2: Distribution of adult sizes (estimated as natural-log-transformed [LN] wet weight [g]) according to fertilization mode for three phyla. Dark gray and light gray points represent data for individual species, and black points represent outliers. Note that scales differ among panels.

in annelids and echinoderms, respectively, but the opposite is true in mollusks—internal fertilizers are 2.8 times larger than external fertilizers (table S5). These patterns are consistent with our overall results for the phyla for which we had higher replication (annelids and echinoderms) but not for mollusks, where the result is based on two genera and five species. Therefore, we are inclined to treat our result in regard to within-genus patterns in mollusks with caution until additional data on body sizes in this group can be assembled for a more representative sample.

Fertilization Mode and Offspring Size versus Adult Size

Adult size increases with offspring size over and above the effects of fertilization mode (offspring size: $F_{1,990} = 6.06$, $P = .01$; fig. 3), but patterns in mollusks are stronger than those in the other two phyla (tables S2, S3).

Fertilization Mode and Developmental Mode versus Adult Size

Developmental mode affects the strength of the relationship between fertilization mode and body size (fertilization × development: $F_{2,1,226} = 3.63$, $P = .03$; fig. 4). In all developmental modes, external fertilizers are still larger than internal fertilizers, but this effect is greatest in planktonic nonfeeding developers, least in aplanktonic developers, and intermediate in planktonic feeding developers (fig. 4). Relative to internal fertilizers, external fertilizers are 9.6, 8.4, and 2.3 times larger than internal fertilizers for species with planktonic nonfeeding, planktonic feeding, and aplanktonic development, respectively (tables S2, S3).

Summary

Fertilization mode covaries strongly and consistently with adult body size—external fertilizers are larger than internal fertilizers. Adult size increases with offspring size, but patterns in mollusks are stronger than those in the other two phyla. Developmental mode influences the strength of the relationship between fertilization mode and body size—external fertilizers are much larger than internal fertilizers in species with planktonic offspring development relative to species with aplanktonic development.

Discussion

Within three phyla (two protostomes and one deuterostome), we observe strong and consistent associations between body size and fertilization mode: external fertilizers are larger than internal fertilizers. This finding suggests that the association between fertilization mode
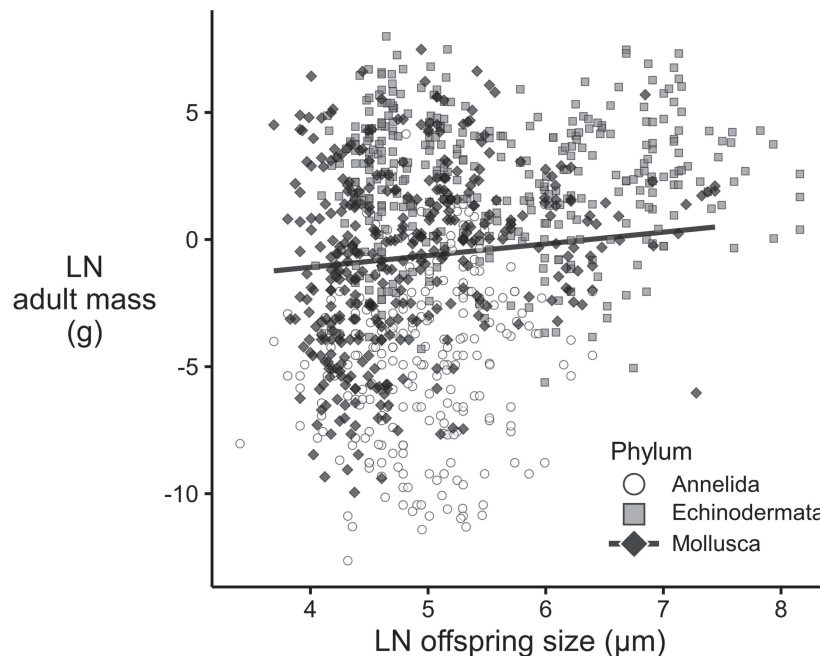

Figure 3: Relationship between adult size (estimated as natural-log-transformed [LN] wet weight [g]) and offspring size (estimated as natural-log-transformed egg diameter) for three phyla. Points represent raw data for each species, and the linear fit represents the significant relationship from phylogenetically controlled regressions in mollusks.
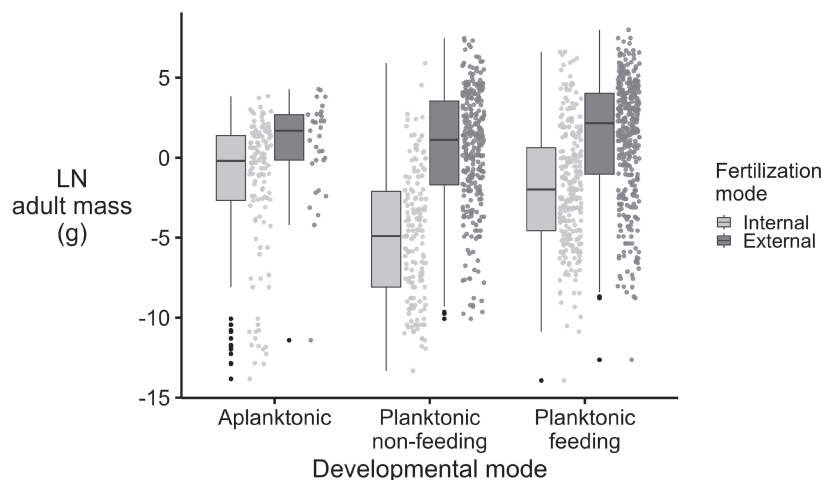
Figure 4: Distribution of adult sizes (estimated as natural-log-transformed [LN] wet weight [g]) according to fertilization mode and developmental mode for all three phyla combined. Dark gray and light gray points represent data for individual species, and black points represent outliers. The outlying points for small (LN −15 to −10 g) aplanktonic developers are all species of annelids, which are generally smaller than the echinoderms and mollusks in our dataset.

and body size is fundamental and ubiquitous, broadening our view of the relationship between fertilization mode and an organism's biology more generally. For example, because body size is such a fundamental feature of an organism, our results allow us to predict how fertilization mode should covary with other well-known correlates of size.

Consequences of Fertilization Mode for Other Traits

Variation in body size drives widespread and repeated patterns across the tree of life (Peters 1983; Reiss 1989; Calder 1996; Hatton et al. 2019; Marshall et al. 2021). Relative to smaller organisms, larger organisms have lower population growth rates (Fenchel 1974; Blueweiss et al. 1978; Savage et al. 2004), lower carrying capacities (Damuth 1981), longer life spans (Speakman 2005), and increased fecundity (Honěk 1993; Visman et al. 1996; Barneche et al. 2018). The association between fertilization mode and body size therefore implies that fertilization mode also covaries with these other traits, such that we should be able to predict much of a species' life history and ecology on the basis of its fertilization mode alone. For example, within any one clade, we would expect a species with external fertilization (and thus a larger body size) to also have a lower population growth rate, lower carrying capacity, and higher fecundity than a congeneric internal fertilizer.

Life history models predict that fertilization mode should vary with resource state (Williams et al. 2005). Accordingly, we find that fertilization mode covaries with resource availability (i.e., body size), but resource availability is only one component of resource state—rates of resource use (i.e.,

metabolic rate) also determine resource state (White et al. 2022). It will therefore be interesting to determine whether metabolic rate (controlling for body size) also covaries with fertilization mode.

Correlation Does Not Equal Causation But . . .

It is tempting to think that one trait might be driving the evolution of the other, but correlational approaches such as ours cannot determine evolutionary chains of causality. Although the patterns we observed are consistent with theory (Henshaw et al. 2014), the ultimate drivers of body size are unclear. We suspect that Henshaw et al.'s (2014) argued sequence of events is likely, that a reduction in body size precedes the evolution of internal fertilization via the following steps: (1) a reduction in body size results in smaller testes (and thus lower sperm production), leading to sperm limitation; (2) sperm limitation favors the production of larger eggs, which are larger targets for sperm; (3) production of larger eggs (and thus fewer of them) favors the retention of eggs to increase fertilization success and egg survival; and (4) egg retention favors the development of anatomy and sperm traits required for internal fertilization. Such a scenario remains speculative however, and we remain open to alternative explanations.

Implications for Latitude, Offspring Size, and Developmental Mode

Despite classic expectations that latitude, offspring size, and developmental mode should covary with body size, the influence of these predictors is far less consistent and far

weaker than that of fertilization mode. Nevertheless, our findings are congruent with other studies of interspecific patterns in ectotherm body size: we found no covariance between body size and latitude (Hawkins and Lawton 1995; Porter and Hawkins 2001; Berke et al. 2013; Moss et al. 2016; but see Olalla-Tárraga and Rodríguez 2007; Womack and Bell 2020; Bansal and Thaker 2021; Campbell et al. 2021), a positive covariance between body size and offspring size (Neuheimer et al. 2015; Rollinson and Rowe 2015, 2016; Olsson et al. 2016; Rollinson et al. 2019; but see Visman et al. 1996), and a tendency for species with aplanktonic/direct development to have smaller body sizes than species with larval development (Strathmann and Strathmann 1982; Chaffee and Lindberg 1986; Hendler and Littman 1986; McHugh 1993; Rouse and Fitzhugh 1994; Giangrande 1997; Webb et al. 2009; Womack and Bell 2020). It will be interesting to see whether the patterns we observe here apply more generally to other taxa. For example, marine rockfishes (Scorpaenidae) include species with all combinations of spawning and fertilization modes (Haldorson and Love 1991; Muñoz 2010), so unlike other fishes, a "clean" test of how fertilization mode covaries with body size seems possible in this group.

Limitations of Database

As with any compilation of this kind, there are limitations in our dataset (see also Marshall et al. 2012; Monro and Marshall 2015). For instance, relative to coastal regions in the global south (particularly Africa and South America), species from the United States, Europe, and Australia are overrepresented in our dataset. Taxonomically, a large portion (40%) of the mollusks in our dataset are sea slugs (which combine exclusively internal fertilization, small body size, and small offspring size), with relatively few (19%) bivalves, so although the patterns we observe in mollusks are largely consistent with the other two phyla, they may not represent mollusks more generally. However, we would expect these types of taxonomic biases to be minimized by our phylogenetic analyses.

We did not differentiate body size measurements between adult males and females because this level of detail was rarely reported in the literature. Consequently, if there is sexual size dimorphism in any of these lineages, nonrandom sampling of body sizes for males versus females could add variation to our dataset and analyses. Nevertheless, that we find consistent patterns regardless of this distinction suggests that the covariance between body size and fertilization mode is strong and unbiased in our dataset. Whether sexual size dimorphism affects our results is unclear—more detailed information on the sex of study organisms is needed to answer this question.

Conclusions

Using a phylogenetically controlled approach, we tested whether fertilization mode covaries with adult body size across three phyla. Our findings support theoretical predictions (Henshaw et al. 2014) and long-standing hypotheses (Strathmann and Strathmann 1982; Hendler and Littman 1986; Rouse and Fitzhugh 1994; Hart et al. 1997; Kupriyanova et al. 2001; McFadden et al. 2001) that external fertilizers should be larger than internal fertilizers. Overall, our results broaden our understanding of how the covariance between fertilization mode and body size shapes the biology of organisms and suggest that the ecological and evolutionary consequences of this covariance may be more profound than has been appreciated previously.

Statement of Authorship

D.J.M. and G.C.J. conceived the study. G.C.J. compiled and standardized the dataset. G.C.J. analyzed the data. G.C.J. wrote the first draft of the manuscript. Both authors contributed substantially to revisions.

Data and Code Availability

Data and code have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.n5tb2rc00; Jarvis et al. 2023).

Literature Cited

Abe, T., and H. Munehara. 2009. Adaptation and evolution of reproductive mode in copulating cottoid species. Pages 221–246 *in* B. G. M. Jamieson, ed. Reproductive biology and phylogeny of fishes. Vol. 8B. CRC, Boca Raton, FL.

Akaike, H. 1978. A Bayesian analysis of the minimum AIC procedure. Annals of the Institute of Statistical Mathematics 30:9–14.

Bansal, U., and M. Thaker. 2021. Diet influences latitudinal gradients in life-history traits, but not reproductive output, in ectotherms. Global Ecology and Biogeography 30:2431–2441.

Barneche, D. R., D. R. Roberston, C. R. White, and D. J. Marshall. 2018. Fish reproductive-energy output increases disproportionately with body size. Science 360:642–645.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bergmann, K. G. L. C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 3:595–708.

Berke, S. K., D. Jablonski, A. Z. Krug, K. Roy, and A. Tomasovych. 2013. Beyond Bergmann's rule: size-latitude relationships in marine Bivalvia world-wide. Global Ecology and Biogeography 22:173–183.

Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. Oecologia 37:257–272.

Bode, M., and D. J. Marshall. 2007. The quick and the dead? sperm competition and sexual conflict in sea. Evolution 61:2693–2700.

Brey, T., C. Müller-Wiegmann, Z. M. C. Zittier, and W. Hagen. 2010. Body composition in aquatic organisms—a global data bank of relationships between mass, elemental composition and energy content. Journal of Sea Research 64:334–340.

Britton, T., C. L. Anderson, D. Jacquet, S. Lundqvist, and K. Bremer. 2007. Estimating divergence times in large phylogenetic trees. Systematic Biology 56:741–752.

Calder, W. A. 1996. Size, function, and life history. Harvard University Press, Cambridge, MA.

Campbell, M. D., D. S. Schoeman, W. Venables, R. Abu-Alhaija, S. D. Batten, S. Chiba, F. Coman, et al. 2021. Testing Bergmann's rule in marine copepods. Ecography 44:1283–1295.

Chaffee, C., and D. R. Lindberg. 1986. Larval biology of Early Cambrian molluscs: the implications of small body size. Bulletin of Marine Science 39:536–549.

Charney, N. D., J. J. Castorino, M. J. Dobro, and S. L. Steely. 2014. Embryo development inside female salamander (*Ambystoma jeffersonianum-laterale*) prior to egg laying. PLoS ONE 9:e91919.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699–700.

Day, T., and P. D. Taylor. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. American Naturalist 149:381–393.

———. 2000. A generalization of Pontryagin's maximum principle for dynamic evolutionary games among relatives. Theoretical Population Biology 57:339–356.

Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. McGraw-Hill, New York.

Eastman, J. M., L. J. Harmon, and D. C. Tank. 2013. Congruification: support for time scaling large phylogenetic trees. Methods in Ecology and Evolution 4:688–691.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Fenchel, T. M. 1974. Intrinsic rate of natural increase: the relationship with body size. Oecologia 14:317–326.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. Sage, Thousand Oaks, CA.

Franzén, Å. 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zoologiska Bidrag Uppsala 31:355–482.

———. 1970. Phylogenetic aspects of the morphology of spermatozoa and spermiogenesis. Pages 29–45 in B. Baccetti, ed. Comparative spermatology. Academic Press, Rome, NY.

———. 1977. Sperm structure with regard to fertilization biology and phylogenetics. Verhandlungen der Deutschen Zoologischen Gesellschaft 70:123–138.

Garland, T., and A. R. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155:346–364.

Giangrande, A. 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. Pages 323–386 in R. N. Gibson and M. Barnes, eds. Oceanography and marine biology: an annual review. Vol. 35. CRC, Boca Raton, FL.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society B 326:119–157.

Gross, M. R., and R. Shine. 1981. Parental care and mode of fertilization in ectothermic vertebrates. Evolution 35:775–793.

Haldorson, L., and M. Love. 1991. Maturity and fecundity in the rockfishes, *Sebastes* spp., a review. Marine Fisheries Review 53:25–31.

Halliday, T. R., and P. A. Verrell. 1984. Sperm competition in amphibians. Pages 487–508 in R. L. Smith, ed. Sperm competition and the evolution of animal mating systems. Academic Press, Orlando, FL.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Hart, M. W., M. Byrne, and M. J. Smith. 1997. Molecular phylogenetic analysis of life-history evolution in asterinid starfish. Evolution 51:1848–1861.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hatton, I. A., A. P. Dobson, D. Storch, E. D. Galbraith, and M. Loreau. 2019. Linking scaling laws across eukaryotes. Proceedings of the National Academy of Sciences of the USA 116:21616–21622.

Hawkins, B. A., and J. H. Lawton. 1995. Latitudinal gradients in butterfly body sizes: is there a general pattern? Oecologia 102:31–36.

Hendler, G., and B. S. Littman. 1986. The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars. Coral Reefs 5:31–42.

Henshaw, J. M., D. J. Marshall, M. D. Jennions, and H. Kokko. 2014. Local gamete competition explains sex allocation and fertilization strategies in the sea. American Naturalist 184:E32–E49.

Hinchliff, C., S. Smith, J. Allman, J. G. Burleigh, R. Chaudhary, L. Cognill, K. Crandall, et al. 2015. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. Proceedings of the National Academy of Sciences of the USA 112:12764–12769.

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66:483–492.

Ives, A. R. 2018. Mixed and phylogenetic models: a conceptual introduction to correlated data. Leanpub, Victoria, Canada.

Jarvis, G. C., and D. J. Marshall. 2023. Data from: Fertilization mode covaries with body size. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.n5tb2rc00.

Kahrl, A. F., R. R. Snook, and J. L. Fitzpatrick. 2021. Fertilization mode drives sperm length evolution across the animal tree of life. Nature Ecology and Evolution 5:1153–1164.

Kumar, S., M. Suleski, J. M. Craig, A. E. Kasprowicz, M. Sanderford, M. Li, G. Stecher, and S. B. Hedges. 2022. TimeTree 5: an expanded resource for species divergence times. Molecular Biology and Evolution 39:msac174.

Kupriyanova, E. K., E. Nishi, H. A. Ten Hove, and A. V Rzhavsky. 2001. Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. Pages 1–101 in R. N. Gibson,

M. Barnes, and R. J. A. Atkinson, eds. Oceanography and marine biology: an annual review. Vol. 39. CRC, Boca Raton, FL.

Levitan, D. R. 1998. Does Bateman's principle apply to broadcast-spawning organisms? egg traits influence in situ fertilization rates among congeneric sea urchins. Evolution 52:1043–1056.

Levitan, D. R., and C. Petersen. 1995. Sperm limitation in the sea. Trends in Ecology and Evolution 10:228–231.

Levitan, D. R., M. A. Sewell, and F.-S. Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecology 73:248–254.

Mank, J. E., D. E. L. Promislow, and J. C. Avise. 2005. Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. Evolution 59:1570.

Marshall, D. J. 2002. In situ measures of spawning synchrony and fertilization success in an intertidal, free-spawning invertebrate. Marine Ecology Progress Series 236:113–119.

Marshall, D. J., P. J. Krug, E. K. Kupriyanova, M. Byrne, and R. B. Emlet. 2012. The biogeography of marine invertebrate life histories. Annual Review of Ecology, Evolution, and Systematics 43:97–114.

Marshall, D. J., M. Malerba, T. Lines, A. L. Sezmis, C. M. Hasan, R. E. Lenski, and M. J. McDonald. 2021. Long-term experimental evolution decouples size and production costs in *Escherichia coli*. Proceedings of the National Academy of Sciences of the USA 119:e2200713119.

Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149:646–667.

McFadden, C. S., R. Donahue, B. K. Hadland, and R. Weston. 2001. A molecular phylogenetic analysis of reproductive trait evolution in the soft coral genus *Alcyonium*. Evolution 55:54–67.

McHugh, D. 1993. A comparative study of reproduction and development in the polychaete family Terebellidae. Biological Bulletin 185:153–167.

Michonneau, F., J. W. Brown, and D. J. Winter. 2016. rotl: an R package to interact with the Open Tree of Life data. Methods in Ecology and Evolution 7:1476–1481.

Millar, R. B., and M. J. Anderson. 2003. The kinetics of monospermic and polyspermic fertilization in free-spawning marine invertebrates. Journal of Theoretical Biology 224:79–85.

Monro, K., and D. J. Marshall. 2015. The biogeography of fertilization mode in the sea. Global Ecology and Biogeography 24:1499–1509.

Moss, D. K., L. C. Ivany, E. J. Judd, P. W. Cummings, C. E. Bearden, W. J. Kim, E. G. Artruc, et al. 2016. Lifespan, growth rate, and body size across latitude in marine Bivalvia, with implications for Phanerozoic evolution. Proceedings of the Royal Society B 283:20161364.

Muñoz, M. 2010. Reproduction in scorpaeniformes. Pages 65–89 *in* K. S. Cole, ed. Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Berkeley.

Neuheimer, A. B., M. Hartvig, J. Heuschele, S. Hylander, T. Kiørboe, K. H. Olsson, J. Sainmont, and K. H. Andersen. 2015. Adult and offspring size in the ocean over 17 orders of magnitude follows two life history strategies. Ecology 96:3303–3311.

Olalla-Tárraga, M. Á., and M. Á. Rodríguez. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. Global Ecology and Biogeography 16:606–617.

Olsson, K. H., H. Gislason, and K. Haste. 2016. Differences in density-dependence drive dual offspring size strategies in fish. Journal of Theoretical Biology 407:118–127.

Page, M. J., J. E. McKenzie, P. M. Bossuyt, I. Boutron, T. C. Hoffmann, C. D. Mulrow, L. Shamseer, et al. 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 372:n71.

Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biological Reviews 45:525–567.

———. 1984. Sperm competition and the evolution of animal mating strategies. Pages 1–60 *in* R. L. Smith, ed. Sperm competition and the evolution of animal mating systems. Academic Press, Orlando, FL.

Parker, G. A., and T. Pizzari. 2010. Sperm competition and ejaculate economics. Biological Reviews 85:897–934.

Pennell, M. W., J. M. Eastman, G. J. Slater, J. W. Brown, J. C. Uyeda, R. G. Fitzjohn, M. E. Alfaro, et al. 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. Bioinformatics 30:2216–2218.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

Porter, E. E., and B. A. Hawkins. 2001. Latitudinal gradients in colony size for social insects: termites and ants show different patterns. American Naturalist 157:97–106.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Reiss, M. J. 1989. The allometry of growth and reproduction. Cambridge University Press, Cambridge.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Robinson, L. A., S. P. R. Greenstreet, H. Reiss, R. Callaway, J. Craeymeersch, I. De Boois, S. Degraer, et al. 2010. Length-weight relationships of 216 North Sea benthic invertebrates and fish. Journal of the Marine Biological Association of the United Kingdom 90:95–104.

Rohlf, F. J. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. Evolution 55:2143–2160.

Rollinson, N., V. Nilsson-Örtman, and L. Rowe. 2019. Density-dependent offspring interactions do not explain macroevolutionary scaling of adult size and offspring size. Evolution 73:2162–2174.

Rollinson, N., and L. Rowe. 2015. Persistent directional selection on body size and a resolution to the paradox of stasis. Evolution 69:2441–2451.

———. 2016. The positive correlation between maternal size and offspring size: fitting pieces of a life-history puzzle. Biological Reviews 91:1134–1148.

———. 2018. Temperature-dependent oxygen limitation and the rise of Bergmann's rule in species with aquatic respiration. Evolution 72:977–988.

Rouse, G. W., and K. Fitzhugh. 1994. Broadcasting fables: is external fertilization really primitive? sex, size, and larvae in sabellid polychaetes. Zoologica Scripta 23:271–312.

Rouse, G. W., and F. Pleijel. 2006. Reproductive biology and phylogeny of Annelida. 4th ed. Science, Enfield, NH.

RStudio Team. 2022. RStudio: integrated development environment for R. RStudio, Boston. http://www.rstudio.com/.

Satterthwaite, F. E. 1941. Synthesis of variance. Psychometrika 6:309–316.

———. 1946. An approximate distribution of estimates of variance components. Biometrics Bulletin 2:110–114.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. American Naturalist 163:429–441.

Shine, R. 1978. Propagule size and parental care: the "safe harbor" hypothesis. Journal of Theoretical Biology 75:417–424.

Smaers, J. B., and F. J. Rohlf. 2016. Testing species' deviation from allometric predictions using the phylogenetic regression. Evolution 70:1145–1149.

Speakman, J. R. 2005. Body size, energy metabolism and lifespan. Journal of Experimental Biology 208:1717–1730.

Stockley, P., M. J. G. Gage, G. A. Parker, and A. P. Møller. 1996. Female reproductive biology and the coevolution of ejaculate characteristics in fish. Proceedings of the Royal Society B 263:451–458.

———. 1997. Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. American Naturalist 149:933–954.

Strathmann, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific Coast. University of Washington Press, Seattle.

Strathmann, R. R., and M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. American Naturalist 119:91–101.

Styan, C. A. 1998. Polyspermy, egg size, and the fertilization kinetics of free-spawning marine invertebrates. American Naturalist 152:290–297.

Styan, C. A., and A. J. Butler. 2000. Fitting fertilisation kinetics models for free-spawning marine invertibrates. Marine Biology 137:943–951.

Thorson, G. 1950. Reproduction and larval ecology of marine bottom invertebrates. Biological Reviews 25:1–45.

Visman, V., S. Pesant, J. Dion, B. Shipley, and R. H. Peters. 1996. Joint effects of maternal and offspring sizes on clutch mass and fecundity in plants and animals. Ecoscience 3:173–182.

Vogel, H., G. Czihak, P. Chang, and W. Wolf. 1982. Fertilization kinetics of sea urchin eggs. Mathematical Biosciences 58:189–216.

Watt, C., S. Mitchell, and V. Salewski. 2010. Bergmann's rule: a concept cluster? Oikos 119:89–100.

Webb, T. J., E. H. M. Tyler, and P. J. Somerfield. 2009. Life history mediates large-scale population ecology in marine benthic taxa. Marine Ecology Progress Series 396:293–306.

White, C. R., L. A. Alton, C. L. Bywater, E. J. Lombardi, and D. J. Marshall. 2022. Metabolic scaling is the product of life-history optimization. Science 377:834–839.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer, New York.

Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, NJ.

Williams, P. D., T. Day, and E. Cameron. 2005. The evolution of sperm-allocation strategies and the degree of sperm competition. Evolution 59:492–499.

Womack, M. C., and R. C. Bell. 2020. Two-hundred million years of anuran body-size evolution in relation to geography, ecology and life history. Journal of Evolutionary Biology 33:1417–1432.

Wootton, R. J., and C. Smith. 2014. Reproductive biology of teleost fishes. Wiley-Blackwell, Oxford.

Xu, S., Z. Dai, P. Guo, X. Fu, S. Liu, L. Zhou, W. Tang, et al. 2021. ggtreeExtra: compact visualization of richly annotated phylogenetic data. Molecular Biology and Evolution 38:4039–4042.

Yu, G. 2022. Data integration, manipulation and visualization of phylogenetic trees. Chapman & Hall/CRC, Boca Raton, FL.

Yu, G., D. K. Smith, H. Zhu, Y. Guan, and T. T. Y. Lam. 2017. ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. Methods in Ecology and Evolution 8:28–36.

References Cited Only in the Online Enhancements

Bishop, J. D. D., and A. J. Pemberton. 2006. The third way: spermcast mating in sessile marine invertebrates. Integrative and Comparative Biology 46:398–406.

Olsen, K. C., W. H. Ryan, A. A. Winn, E. T. Kosman, J. A. Moscoso, S. A. Krueger-Hadfield, S. C. Burgess, et al. 2020. Inbreeding shapes the evolution of marine invertebrates. Evolution 74:871.
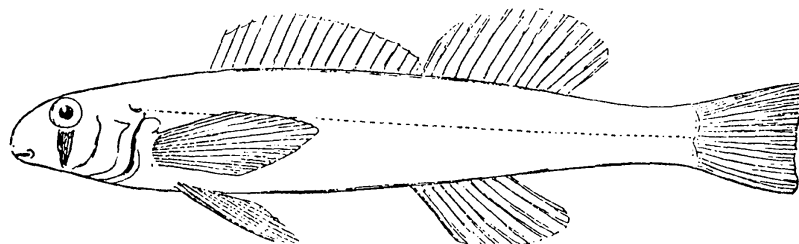
"The most simply beautiful of all fresh-water fishes is the green-sided darter (*Diplesium blennioides*; [figured is] a species of this genus). He is not, like the Pœcilichthys, an animated rainbow, but has the beauty of green grass, wild violets, or a log covered with green moss." From "Johnny Darters" by D. S. Jordan and H. E. Copeland (*The American Naturalist*, 1876, 10:335–341).