

# Eggs as Energy: Revisiting the Scaling of Egg Size and Energetic Content Among Echinoderms

A. L. MORAN\*, J. S. McALISTER†, AND E. A. G. WHITEHILL

*Department of Biological Sciences, 132 Long Hall, Clemson University, Clemson, South Carolina 29631*

**Abstract.** Marine organisms exhibit substantial life-history diversity, of which egg size is one fundamental parameter. The size of an egg is generally assumed to reflect the amount of energy it contains and the amount of per-offspring maternal investment. Egg size and energy are thought to scale isometrically. We investigated this relationship by updating published datasets for echinoderms, increasing the number of species over those in previous studies by 62%. When we plotted egg energy *versus* egg size in the updated dataset we found that planktotrophs have a scaling factor significantly lower than 1, demonstrating an overall trend toward lower energy density in larger planktotrophic eggs. By looking within three genera, *Echinometra*, *Strongylocentrotus*, and *Arbacia*, we also found that the scaling exponent differed among taxa, and that in *Echinometra*, energy density was significantly lower in species with larger eggs. Theoretical models generally assume a strong tradeoff between egg size and fecundity that limits energetic investment and constrains life-history evolution. These data suggest that the evolution of egg size and egg energy content can be decoupled, possibly facilitating response to selective factors such as sperm limitation which could act on volume alone.

## Introduction

Eggs are remarkable cells because of their capacity to develop, through regulation, into embryos and larvae (Brusca *et al.*, 1997; Grosberg and Strathmann, 1998; Mtango *et al.*, 2008). In many marine invertebrate taxa whose gametes or newly fertilized zygotes are freely spawned into the

plankton, development progresses without maternal or paternal direction or energy beyond what is invested in the egg through oogenesis (McEdward, 1996; Luttikhuizen *et al.*, 2011). Eggs must therefore contain not only information to initiate and regulate the process of embryogenesis, and compounds that protect gametes and embryos from stressors (*e.g.*, Adams and Schick, 1996; Thomas *et al.*, 2001; Hand and Honek, 2005), but also materials to build embryos, such as proteins, carbohydrates, and structural (polar) lipids, along with energetic (neutral) lipids as energy to fuel developmental processes. Eggs are generally supplied with numerous yolk granules to serve these purposes, and the amount and distribution of yolk varies tremendously and of itself affects many aspects of development (Brusca *et al.*, 1997; Gilbert, 2006). The energy contained in yolk and the other maternally loaded molecules in an egg, along with accessory structures and the metabolic cost of oogenesis (which is rarely considered), equals the total investment that most free-spawners make in a single offspring. The energetic cost to the mother of producing a single egg drives a fundamental trade-off between the number of ova an individual can produce and the quality of those offspring (Smith and Fretwell, 1974). Thus, egg composition and energy are driven by top-down selective forces acting at many levels of an organism's life history, from the egg itself, to embryos, larvae, juveniles, and adults. Bottom-up factors at the physiological, biochemical, and ecological levels are doubtlessly important as well, though they are not as well understood (Moran and McAlister, 2009).

The size of the egg has long been used as a simple means of estimating energy and maternal investment; size, through its correlation with energy, plays an important role in the conceptual framework used to understand the evolution of life histories of marine organisms (Thorson, 1950; Vance, 1973). Large egg size is correlated with many life-history traits that reflect increases in egg energy (Strathmann,

Received 17 January 2013; accepted 31 May 2013.

\* To whom correspondence should be addressed. E-mail: morana@hawaii.edu. Current address: Department of Biology, University of Hawaii at Manoa, Honolulu, HI 96822.

† Current address: Department of Biology, College of the Holy Cross, 1 College Street, Worcester, Massachusetts 01610.

1985), including larval size and shape (McEdward, 1986), larval feeding mode (Strathmann, 1985), length of larval development (Thorson, 1950; Vance, 1973; Strathmann, 1985; but see Mercier *et al.*, 2013, for a discussion of possible exceptions), and postzygotic survival (Strathmann, 1985) (reviewed in Moran and McAlister, 2009). One potential drawback to using egg size as a predictor of these life-history traits, however, is that if selection can act on size and egg composition separately, then size and energy can be uncoupled (McAlister and Moran, 2012). As one example, fertilization occurs externally for many marine organisms, and larger eggs provide better targets for sperm and therefore have higher fertilization rates (Levitan, 1993, 1996; Podolsky and Strathmann, 1996). There is considerable evidence to suggest that when sperm are limiting, selection will favor females that produce larger eggs (Levitan, 1993; Levitan and Irvine, 2001; Farley and Levitan, 2001). However, if egg energy content scales isometrically with egg size, then doubling the volume of an egg also doubles its energetic cost; all else being equal, doubling egg volume would halve the number of offspring a mother could produce, reducing the fitness benefit of increased fertilization success (Jaekle, 1995; Podolsky and Strathmann, 1996; McEdward and Morgan, 2001). If, however, larger eggs could be produced at comparatively low cost, this would alleviate constraints on the evolution of egg size imposed by trade-offs between fertilization success and high fecundity (Jaekle, 1995; Podolsky and Strathmann, 1996; Podolsky, 2001, 2004).

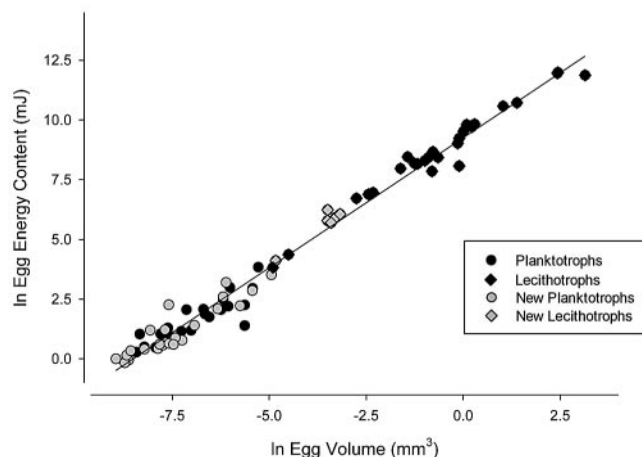
Despite considerable interest in these ideas and the fundamental importance of determining the links between egg size and egg energy, few studies have closely examined the relationship between these traits. Among marine invertebrates, echinoderms are the taxon for which we have the most information on the evolution of larval development in general (Raff and Byrne, 2006) and the scaling of egg energy with egg size in particular. A broad, frequently cited series of meta-analyses that examined egg energetic content in echinoderms suggests that in this group, energy content scales isometrically with egg volume across five orders of magnitude in egg volumes (Jaekle, 1995; with additions by Sewell and Manahan, 2001, and McEdward and Morgan, 2001). These data, collected using an assortment of biochemical methods, spanning 5 orders of magnitude in egg volume, and representing different life-history strategies and taxonomic groups within Echinodermata, suggest that egg energy density remains largely the same regardless of egg volume, even in the face of different regression models and different assumptions for calculating egg energy (McEdward and Morgan, 2001). Most models of egg size evolution have assumed this scaling relationship either explicitly (Jaekle, 1995; Podolsky and Strathmann, 1996; Levitan, 2000; McEdward and Morgan, 2001; Podolsky, 2001, 2004) or implicitly (Farley and Levitan, 2001; Levi-

tan, 2006). Our goals in this study were to reexamine the scaling of egg size and energy in light of the expanding amount of new data available and to closely examine subsets of the data to evaluate the evidence for the adaptive coupling of egg size and egg energy in a phylogenetic context. In particular, we ask (1) whether scaling relationships differ between planktotrophic species, which must feed to reach metamorphosis, and lecithotrophic species, which can reach metamorphosis without particulate food; (2) whether scaling relationships vary when looking within closely related taxa; and (3), in light of these questions, whether egg size and egg energy are mechanistically or evolutionarily linked.

### Data Collection and Analysis

We calculated scaling exponents by plotting egg energy against egg size, using all available data from echinoderms. These included data from 47 species used in McEdward and Morgan (2001) and published data from 29 species not included in this analysis (see Appendix). For simplicity, we used the energy and volume data from table 1 in McEdward and Morgan (2001), which for some species had been corrected, for example, for missing carbohydrate measurements, the “remainder fraction” (calculated in a variety of ways, depending on the original study), or for multiple measurements made by different authors on particular species. We did not apply corrections for missing carbohydrate or the “remainder fraction” to the 29 new species in our dataset because (1) the magnitude and even the existence of that fraction is difficult to establish (see Moran and McAlister, 2009, for discussion), and (2) McEdward and Morgan (2001) found that different methods for estimating energy yielded the same scaling relationships, concluding that “analyses of scaling are robust to details of the data and differences among studies.”

For 5 of the 29 new species (not included in McEdward and Morgan, 2001), the data in the Appendix were collected by the authors and are presented here for the first time. Methods for spawning, egg size measurement, and biochemical analyses of these additional species can be found in McAlister and Moran (2012); species, collection localities, and sample sizes are included. Egg sizes and egg energies, methods for estimating energy content, and source material for all other species are also included. For 7 of the 76 species, egg volume and content were measured in more than one study. When that was the case, we averaged volume and energy values among studies and used the average values for the regression analysis. We analyzed all the data combined and then broke the dataset into two groups on the basis of developmental mode (planktotrophs separate from lecithotrophs). We included the single facultative planktotroph, *Clypeaster rosaceus*, with the lecithotrophs; the regression parameters for lecithotrophs were



**Figure 1.** Plot of ln egg energy content (mJ) versus ln egg volume ( $\text{mm}^3$ ) for all echinoderm data combined ( $n = 76$  species). Circles represent planktotrophic species; diamonds represent lecithotrophic species. Black symbols indicate species included in McEdward and Morgan (2001) ( $n = 47$ ); gray symbols indicate species that are new to this study ( $n = 29$ ). Scaling exponent of all data combined = 1.09,  $r^2 = 0.98$ .

unchanged (to 2 decimal points) by its inclusion or exclusion. Among planktotrophs, we also separately examined the relationship between egg energy and egg size within three genera for which there were three or more species represented (*Arbacia*, *Echinometra*, and *Strongylocentrotus*). Linear regression (SigmaPlot ver. 12, SysStat Software, Inc.) was used to calculate scaling exponents and goodness of fit ( $r^2$ ) from log-log transformed data (Jaekle, 1995). Although many regression models are available, we chose to log-transform both axes (equivalent to a power function) to make our scaling exponents and goodness of fit estimates easily comparable to previous work (e.g., Strathmann and Vedder, 1977; Jaekle, 1995; Sewell and Manahan, 2001). McEdward and Morgan (2001) advocated using a full allometric model rather than power functions (equivalent to using log-log transformed data) because the allometric model is more general in that it is not constrained to pass through the origin; however, they found only minor (“negligible”) differences between the scaling relationships and goodness of fit estimates of the two models, and the egg energy/egg volume relationship can be logically inferred to pass through the origin. Deviation of scaling exponent slope from a slope of 1.0 was tested using GraphPad Prism 6.

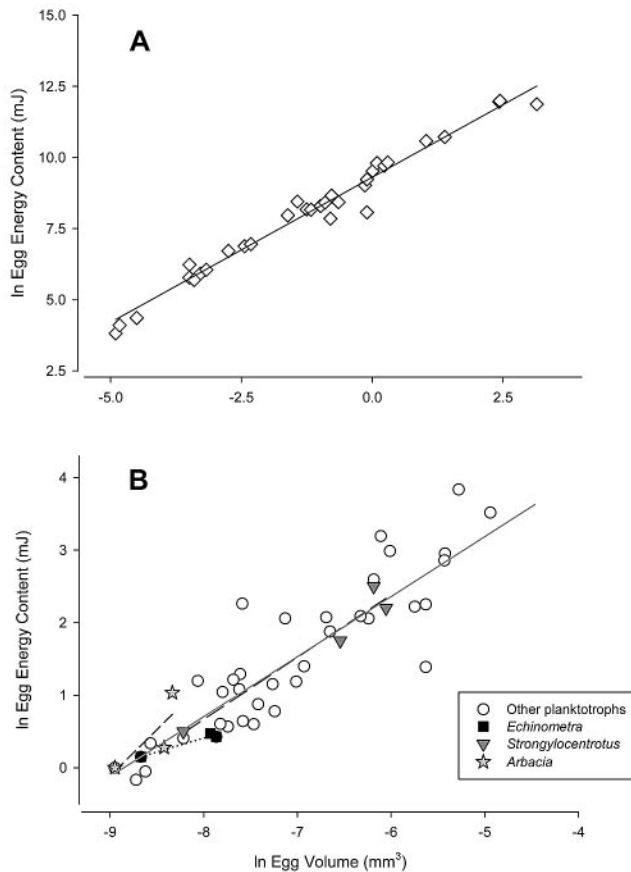
## Results and Discussion

Our addition of 29 taxa to the dataset from McEdward and Morgan (2001), while it increased the total number of species by 62%, made no measureable difference in the overall scaling exponent; the slope of the line regressing egg energy on size for all 76 species combined was 1.09 ( $r^2 = 0.98$ ) (Fig. 1), identical to the results from the McEdward

and Morgan’s (2001) original, smaller dataset. On its face, this result appears to support Jaekle’s (1995) conclusion that “free-spawned echinoderm eggs are proportionately identical, i.e., all characters scale to egg volume $^{-1.0}$ .” However, in our expanded dataset the overall scaling exponent, while the same as McEdward and Morgan’s, was significantly greater than 1 ( $P < 0.0001$ ,  $df = 74$ ), indicating that with larger sample sizes, energy density in fact increases with size across all echinoderms. This means that larger eggs contain proportionately more energy than smaller eggs, and suggests that across taxa, the production of larger eggs comes at a disproportionately large cost to fecundity. However, the broad dataset contains a tremendous 5-orders-of-magnitude range in egg volumes and combines both planktotrophic and lecithotrophic taxa. A closer look at the data shows that the overall scaling exponent is likely driven in part by the different volumes and energy densities between planktotrophs and lecithotrophs.

As Jaekle (1995) also pointed out, energy density (the amount of energy per unit volume) varies between planktotrophs and lecithotrophs, and the scaling of energy and size differs between the two developmental modes. In our expanded dataset with six new lecithotrophic species, the scaling exponent for lecithotrophs changed only slightly (scaling exponent = 1.03,  $r^2 = 0.97$ ), and it was not significantly different from 1 ( $P = 0.363$ ,  $df = 30$ ; Fig. 2A). For planktotrophic species, however, in the expanded dataset the scaling exponent was 0.86 (Fig. 2;  $r^2 = 0.81$ ), significantly lower than 1.0 ( $P = 0.016$ ,  $df = 42$ ) and significantly different from the scaling exponent of lecithotrophs ( $F$ -test:  $F = 6.15$ ,  $df$  numerator = 1,  $df$  denominator = 72,  $P = 0.015$ ) (Fig. 2B). With these additional data, it is now evident that the two modes have differing relationships between volume and energy, and that among planktotrophs, egg energy density decreases with increasing egg size. In both earlier analyses (Jaekle, 1995) and our expanded dataset, the energy density of lecithotrophic eggs was significantly higher than that of planktotrophic eggs ( $11.23 \pm 0.61$  (SE) vs.  $5.91 \pm 0.46$  mJ/nl for the two developmental modes, respectively; Student’s 2-tailed  $t$  test,  $df = 74$ ,  $t = 7.0746$ ,  $P < 0.001$ ). Because lecithotrophic eggs are both larger and more energy dense than planktotrophic eggs, the overall greater-than-isometric scaling in the combined dataset may derive from pooling data from the two developmental modes.

McEdward and Morgan (2001) found that in their smaller dataset, one species, *Notasterias armatus*, had potential to strongly influence the data; it was not, however, identified as an outlier or as having strong leverage in the expanded dataset (Systat 11.0, Systat, Inc.), and no other species had strong leverage in the total dataset or in planktotrophs and lecithotrophs separately. *Encope aberrans* was identified as an outlier in the combined dataset (Studentized residual =  $-4.2$ ) and in the planktotrophs alone (Studentized resid-



**Figure 2.** (A) Plot of ln egg energy (mJ) versus ln egg volume ( $\text{mm}^3$ ) for the 32 lecithotrophic species alone. Scaling exponent = 1.03,  $r^2 = 0.97$ . (B) Plot of ln egg energy content (mJ) versus ln egg volume ( $\text{mm}^3$ ) for the 44 planktotrophic species alone. Scaling exponent = 0.86,  $r^2 = 0.81$  (solid gray line) ( $n = 44$ ). Scaling exponent = 0.38,  $r^2 = 0.96$  for *Echinometra* ( $n = 3$ ) (black squares, dotted line). Scaling exponent = 0.86,  $r^2 = 0.95$  for *Strongylocentrotus* ( $n = 4$ ) (gray triangles, long dashed line). Scaling exponent = 1.28,  $r^2 = 0.63$  for *Arbacia* ( $n = 3$ ) (gray stars, medium dashed line).

ual =  $-3.42$ ); *Perknaster fuscus* was an outlier in the lecithotrophic dataset (Studentized residual =  $-3.9$ ). When we removed these outliers and ran regressions on the remaining data, the slopes and goodness-of-fit did not change substantially; for the combined dataset, the slope was the same to 2 decimal places (1.09) and the  $r^2$  increased from 0.97 to 0.98. Among planktotrophs, the slope and goodness-of-fit changed from 0.86 to 0.90 and from 0.81 to 0.85, respectively; for lecithotrophs, removing the outlier changed the slope from 1.03 to 1.04 and the goodness-of-fit from 0.97 to 0.98. Excluding the outliers did not change the significance of any of the comparisons of slopes described above, suggesting the relationships between egg size and energy are robustly different among developmental modes even when individual species diverge from the general pattern.

Generally, the energy density of eggs could differ among

taxa by two mechanisms (or some combination of the two). First, lower-density eggs might be constructed from less-energy-rich materials (Podolsky, 2004); that is, they might have greater proportions of protein (24 kJ/g) or carbohydrate (17.5 kJ/g) compared to lipid (39.5 kJ/g) (energetic values from Gnaiger, 1983). Differences in composition appear to underlie much of the difference between planktotrophs and lecithotrophs, since planktotrophs, which are less energy-dense overall, are also proportionally protein- and carbohydrate-rich (Jaekle, 1995; Prowse *et al.*, 2008). The greater protein densities of most planktotrophic eggs might be due to selection for rapid development, which could lead to greater amounts of maternally-loaded proteins in oocytes (Jaekle, 1995); this seems an unlikely explanation, however, because there is no difference in the rate at which lecithotrophs and planktotrophs develop to the swimming stage, and egg size is not correlated with cell-cycle duration among marine invertebrates (Staver and Strathmann, 2002; Strathmann *et al.*, 2002). Alternatively, lecithotrophs might contain proportionately more lipid because, unlike planktotrophs, they cannot feed to build lipid stores during development but must load lipids into the egg to fuel metamorphosis and early post-metamorphic development (Emlet *et al.*, 1987; Prowse *et al.*, 2008). Indeed, lecithotrophs generally contain proportionately more lipid than planktotrophs (Jaekle, 1995; Prowse *et al.*, 2008), and the roles of egg lipids may differ between the two modes of development. The neutral lipid stores of planktotrophic eggs (triacylglycerols) fuel early morphogenesis, and when larvae are not fed, are often entirely depleted by the end of morphogenesis (Sewell, 2005; Meyer *et al.*, 2007; Byrne *et al.*, 2008; Whitehill and Moran, 2012). In lecithotrophs, part of the egg lipid goes to fuel morphogenesis, larval metabolism, and metamorphosis, while the rest (including other lipid classes that are lacking in planktotrophs, such as diacylglycerols) may be carried over into the juvenile stage (Emlet and Hoegh-Guldberg, 1997; Byrne and Cerra, 2000; Byrne *et al.*, 2003, 2008; Prowse *et al.*, 2008). Among lecithotrophs, therefore, the evolution of large, energy-dense eggs may reflect selection not just to fuel larval morphogenesis, but also to supply the metamorphic and post-metamorphic animal with energy (Byrne *et al.*, 2003).

Within planktotrophs, however, as egg size increases egg energy density decreases, such that larger eggs contain proportionally less energy than small eggs. This overall pattern does not appear to be due to compositional shifts, because the protein, carbohydrate, and lipid composition of planktotrophic eggs do not change overall with size across all planktotrophs (Jaekle, 1995). Therefore, among planktotrophic species, a second mechanism may underlie changes in the energy density of eggs: larger eggs could contain a higher percentage of water (Podolsky 2004). To test this idea, we looked at the relationship between egg energy and egg size among three planktotrophic sister spe-



cies within the genus *Echinometra* from Central America. These three species, *Echinometra vanbrunti* A. Agassiz, 1863 (eastern Pacific), *E. lucunter* (Linnaeus, 1758) (western Atlantic), and *E. viridis* A. Agassiz, 1863 (western Atlantic), form a geminate cluster and likely separated within the last 4 MY (McCartney *et al.*, 2000). Egg sizes, biochemical compositions, and energy densities of all three species are described in McAlister and Moran (2012); because these data were collected and analyzed by the same researchers during the same time frame and using the same methods for biochemical analysis, the three *Echinometra* species provide a strong framework for intrageneric comparisons despite the small number of species. As in other phyla, egg size differences between geminates are thought to reflect natural selection acting on maternal investment strategies to optimize fitness in the food-poor western Atlantic (large eggs) and the comparatively productive eastern Pacific (small eggs) (Lessios, 1990; Jackson and Cubilia Herrera, 2000; Moran, 2004), at least in part (McAlister and Moran, 2012).

In *Echinometra*, the two western Atlantic species have egg volumes that are roughly double that of their eastern Pacific geminate ( $1.8\times$  for *E. lucunter* and  $2.2\times$  for *E. viridis*), but after summing the energetic values of the major biochemical egg constituents for all three species, the western Atlantic species were substantially lower in energy density ( $\sim 40\%$  and  $\sim 25\%$  lower for *E. viridis* and *E. lucunter*, respectively, compared to *E. vanbrunti*) (McAlister and Moran, 2012). Between the two western Atlantic species, the eggs of *E. viridis* were  $1.2\times$  larger than the eggs of *E. lucunter*, but energy per egg was the same in the two species. The low energy density of eggs of the two western Atlantic species compared to *E. vanbrunti* was likely due to higher water content rather than a decrease in proportional representation of energy-rich lipid. Eggs of *E. lucunter* and *E. viridis*, the two species with the larger eggs, had higher lipid-to-protein ratios (0.5:1 for *E. lucunter* and 0.4:1 for *E. viridis* vs. 0.3:1 for *E. vanbrunti*) and lipid-to-carbohydrate ratios (4.3:1 and 3.5:1 vs. 2.2:1) than did eggs of *E. vanbrunti* (calculated from values in McAlister and Moran, 2012). The two western Atlantic species also had substantially lower energy densities ( $\sim 40\%$  and  $\sim 25\%$  for *E. viridis* and *E. lucunter*, respectively) than did *E. vanbrunti*. The scaling exponent for the relationship between egg energy content and egg volume within *Echinometra* was 0.38 ( $r^2 = 0.96$ , Fig. 2B), significantly lower than 1 ( $P = 0.040$ ,  $df = 1$ ).

Although the egg volume of both western Atlantic species of *Echinometra* is roughly double that of their eastern Pacific counterpart ( $1.8\times$  for *E. lucunter* and  $2.2\times$  for *E. viridis*), because of the low scaling factor, all else being equal, fecundity would be lowered by only 25% for either of the larger-egged species compared to *E. vanbrunti*. Between the two western Atlantic species, the eggs of *E. viridis* were

$1.2\times$  larger than the eggs of *E. lucunter*, but energy per egg was the same in the two species; meaning that from an energetics perspective, *E. viridis* can produce larger eggs than *E. lucunter* with no corresponding decrease in fecundity. Because increased egg size comes at low (or no) cost to fecundity in this genus, natural selection for increased fertilization alone would be sufficient to favor larger eggs in these taxa when sperm are limiting (Podolsky and Strathmann, 1996). Given that the larger egg size of *E. viridis* does not represent greater energy reserves that might enhance larval performance (relative to *E. lucunter*), a scenario of evolution to enhance fertilization success is likely.

The low scaling factor of egg energy and egg size in *Echinometra* suggests that inferences about the evolution of these life-history characters must be made with caution when examining broader, phylum-wide datasets. Selection for increased egg energy may, within planktotrophic species, lead to isometric scaling, assuming that the proportions of lipid, protein, and carbohydrate necessary for building a planktotrophic larva remain constant. But because lipid contains proportionally more energy than protein or carbohydrate (Gnaiger, 1983), it may be that egg energy density decreases with egg size because proportionally less lipid is required to fuel morphogenesis of the feeding larva in larger eggs. This is not the case for *Echinometra*, where the two species with larger eggs have comparatively higher proportions of lipid (McAlister and Moran, 2012). However, little is known about the energetics of morphogenesis or whether there is a predictable relationship between the size and complexity of the prefeeding larva and the amount of energy required to build it. The combined dataset has two other genera with egg energy and egg size data for more than two planktotrophic species. In the first, *Arbacia* ( $n = 3$ ), the scaling exponent was 1.28 ( $r^2 = 0.63$ ) which, though substantially larger than the scaling exponent of *Echinometra*, was not significantly different from 1.0 ( $P = 0.823$ ,  $df = 1$ ). In the second genus, *Strongylocentrotus* ( $n = 4$ ), the scaling exponent was 0.86 ( $r^2 = 0.95$ ), which was similar to the relationship found across all planktotrophs but was not significantly different from 1.0 ( $P = 0.422$ ,  $df = 2$ ) (Fig. 2B).

*Echinometra* may be an unusual case, but the differences in scaling exponents among *Echinometra*, *Arbacia*, and *Strongylocentrotus* show that the relationship between egg energy and egg size, and therefore the strength of size-fecundity tradeoffs, can vary among planktotrophic genera. Therefore, it may not be accurate to assume that the same constraints and trade-offs will apply to the evolution of egg size in all echinoderms, or that selection on egg size based on fertilization success will operate in the same way in all groups. When a robust phylogeny of echinoderms becomes available, phylogenetic analysis may determine if and how patterns of shared evolutionary ancestry affect the overall scaling pattern. Likewise, many of the benefits that are

thought to accrue to larvae from larger eggs—for example, shortened planktonic development, increased postzygotic survival, or both—may not be realized when larger eggs contain proportionally less energy. Finally, although informative on a broad, general level, the isometric scaling relationship of egg volume and egg energy found across echinoderms cannot be used to infer constraints operating on the evolution of egg size at lower taxonomic levels, nor to predict egg energy from egg size over small changes in volume (McEdward and Morgan, 2001). As more egg size and energy data become available from within closely related groups, differences among scaling exponents can be used to gauge the strength of fecundity-size tradeoffs.

### Acknowledgments

We thank S. Crickenberger and D. Levitan for constructive input, and R. Collin, C. Genovese, H. Lessios, L. Geyer, K. McDonald, S. Crickenberger, and the staff of the Smithsonian Tropical Research Institute for logistical support. This work was supported by NSF OCE- 0850764 to ALM.

### Literature Cited

- Adams, N. L., and J. M. Shick. 1996. Mycosporine-like amino acids provide protection against ultraviolet radiation in eggs of the green sea urchin *Strongylocentrotus droebachiensis*. *Photochem. Photobiol.* 64: 149–158.
- Brusca, G. J., R. C. Brusca, and S. F. Gilbert. 1997. Characteristics of metazoan development. Pp. 3–19 in *Embryology: Constructing the Organism*, S. F. Gilbert and A. M. Raunio, eds. Sinauer Associates, Sunderland, MA.
- Byrne, M., and A. Cerra. 2000. Lipid dynamics in the embryos of *Patiriella* species (Asteroidea) with divergent modes of development. *Dev. Growth Differ.* 42: 79–86.
- Byrne, M., P. Cisternas, P. Selvakumaraswamy, J. T. Villinski, and R. R. Raff. 2003. Evolution of maternal provisioning in ophiuroids, asteroids and echinoids. Pp. 171–175 in *Echinoderm Research 2001*, J. P. Feral and B. David, eds. A. A. Balkema, Lisse.
- Byrne, M., T. A. A. Prowse, M. A. Sewell, S. Dworjanyn, J. E. Williamson, and D. Vaitilingon. 2008. Maternal provisioning for larvae and larval provisioning for juveniles in the toxopneustid sea urchin *Triploneustes gratilla*. *Mar. Biol.* 155: 473–482.
- Emlet, R. B., and O. Hoegh-Guldberg. 1997. Effects of egg size on postlarval performance: experimental evidence from a sea urchin. *Evolution* 51: 141–152.
- Emlet, R. B., L. R. McEdward, and R. R. Strathmann. 1987. Echinoderm larval ecology viewed from the egg. Pp. 55–136 in *Echinoderm Studies*, M.J. Jangoux and J.M. Lawrence, eds. Balkema, Rotterdam.
- Falkner, I., M. Byrne, and M. A. Sewell. 2006. Maternal provisioning in *Ophionereis fasciata* and *O. Schayeri*: brittle stars with contrasting modes of development. *Biol. Bull.* 211: 204–207.
- Farley, G. S., and D. R. Levitan. 2001. The role of jelly coats in sperm-egg encounters, fertilization success, and selection on egg size in broadcast spawners. *Am. Nat.* 157: 626–636.
- Gilbert, S. F. 2006. *Developmental Biology*, 8th ed. Sinauer Associates, Sunderland, MA. 722 pp.
- Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. Pp. 337–345 in *Polarographic Oxygen Sensors: Aquatic and Physiological Adaptations*, E. Gnaiger and H. Forstner, eds. Springer-Verlag, New York.
- Grosberg, R. K., and R. R. Strathmann. 1998. One cell, two cell, red cell, blue cell: the persistence of a unicellular stage in multicellular life histories. *Trends Ecol. Evol.* 13: 112–116.
- Hand, C. E., and J. F. Honek. 2005. Biological chemistry of naturally occurring thiols of microbial and marine origin. *J. Nat. Prod.* 68: 293–308.
- Hoegh-Guldberg, O., and R. B. Emlet. 1997. Energy use during the development of a lecithotrophic and a planktotrophic echinoid. *Biol. Bull.* 192: 27–40.
- Jackson, J. B. C., and A. Herrera Cubilia. 2000. Adaptation and constraint as determinants of zooid and ovicell size among encrusting asporophoran cheilostome Bryozoa from opposite sides of the Isthmus of Panama. Pp. 249–258 in *Proceedings of the 11th International Bryozoology Association Conference*, A. Herrera Cubilia and J. B. C. Jackson, eds. 26–31 January 1998. Tropical Research Institute, Balboa, Panama.
- Jaekle, W. B. 1995. Variation in the size, energy content, and biochemical composition of invertebrate eggs: correlates to the mode of larval development. Pp. 49–77 in *Ecology of Marine Invertebrate Larvae*, L. R. McEdward, ed. CRC Press, Boca Raton, FL.
- Lessios, H. A. 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.
- Levitan, D. R. 1993. The importance of sperm limitation to the evolution of egg size in marine invertebrates. *Am. Nat.* 141: 517–536.
- Levitan, D. R. 1996. Predicting optimal and unique egg sizes in free-spawning marine invertebrates. *Am. Nat.* 148: 174–188.
- Levitan, D. R. 2000. Optimal egg size in marine invertebrates: theory and phylogenetic analysis of the critical relationship between egg size and development time in echinoids. *Am. Nat.* 156: 175–192.
- Levitan, D. R. 2006. The relationship between egg size and fertilization success in broadcast-spawning marine invertebrates. *Integr. Comp. Biol.* 46: 298–311.
- Levitan, D. R., and S. D. Irvine. 2001. Fertilization selection on egg and jelly-coat size in the sand dollar *Dendraster excentricus*. *Evolution* 55: 2479–2483.
- Luttikhuisen, P. C., P. J. C. Honkoop, and J. Drent. 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*. *J. Exp. Mar. Biol. Ecol.* 396: 156–161.
- McAlister, J. S., and A. L. Moran. 2012. Relationships among egg size, composition, and energy: a comparative study of geminate sea urchins. *PLoS One* 7: e41599.
- McCartney, M. A., G. Keller, and H. A. Lessios. 2000. Dispersal barriers in tropical oceans and speciation in Atlantic and eastern Pacific sea urchins of the genus *Echinometra*. *Mol. Ecol.* 9: 1391–1400.
- McEdward, L. R. 1986. Comparative morphometrics of echinoderm larvae. II. Larval size, shape, growth, and the scaling of feeding and metabolism in echinoplutei. *J. Exp. Mar. Biol. Ecol.* 96: 267–286.
- McEdward, L. R. 1996. Experimental manipulation of parental investment in echinoid echinoderms. *Am. Zool.* 36: 169–179.
- McEdward, L. R., and K. H. Morgan. 2001. Interspecific relationships between egg size and the level of parental investment per offspring in echinoderms. *Biol. Bull.* 200: 33–50.
- Mercier, A., M. A. Sewell, and J.-F. Hamel. 2013. Pelagic propagule duration and developmental mode: reassessment of a fading link. *Glob. Ecol. Biogeogr.* 22: 517–530.
- Meyer, E., A. J. Green, M. Moore, and D. T. Manahan. 2007. Food availability and physiological state of sea urchin larvae (*Strongylocentrotus purpuratus*). *Mar. Biol.* 152: 179–191.
- Miner, B. G., J. D. Cowart, and L. R. McEdward. 2002. Egg energetics for the facultative planktotroph *Clypeaster rosaceus* (Echinodermata: Echinoidea), revisited. *Biol. Bull.* 202: 97–99.
- Moore, M., and D. T. Manahan. 2007. Variation among females in egg

- lipid content and developmental success of echinoderms from McMurdo Sound, Antarctica. *Polar Biol.* **30**: 1245–1252.
- Moran, A. L. 2004. Egg size evolution in tropical American arcid bivalves: The comparative method and the fossil record. *Evolution* **58**: 2718–2733.
- Moran, A. L., and J. S. McAlister. 2009. Egg size as a life history character of marine invertebrates: is it all it's cracked up to be? *Biol. Bull.* **216**: 226–242.
- Moreno, G., and O. Hoegh-Guldberg. 1999. The energetics of development of three congeneric seastars (*Patiria* Verrill, 1913) with different types of development. *J. Exp. Mar. Biol. Ecol.* **235**: 1–20.
- Mtango, N. R., S. Potireddy, and K. Latham. 2008. Oocyte quality and maternal control of development. *Int. Rev. Cell. Mol. Biol.* **268**: 223–290.
- Podolsky, R. D. 2001. Evolution of egg target size: an analysis of selection on correlated characters. *Evolution* **55**: 2470–2478.
- Podolsky, R. D. 2004. Life-history consequences of investment in free-spawned eggs and their accessory coats. *Am. Nat.* **163**: 735–753.
- Podolsky, R. D., and R. R. Strathmann. 1996. Evolution of egg size in free-spawners: consequences of the fertilization-fecundity trade-off. *Am. Nat.* **148**: 160–173.
- Poorbagher, H., M. D. Lamare, and M. F. Barker. 2010a. The relative importance of parental nutrition and population versus larval diet on development and plasticity of *Sclerasterias mollis* larvae. *J. Mar. Biol. Assoc. UK* **90**: 527–536.
- Poorbagher, H., M. D. Lamare, M. F. Barker, and W. Rayment. 2010b. Relative importance of parental diet versus larval nutrition on development and phenotypic plasticity of *Pseudechinus huttoni* larvae (Echinodermata: Echinoidea). *Mar. Biol. Res.* **6**: 302–314.
- Prowse, T. A. A., M. A. Sewell, and M. Byrne. 2008. Fuels for development: evolution of maternal provisioning in asterinid sea stars. *Mar. Biol.* **153**: 337–349.
- Raff, R. A., and M. Byrne. 2006. The active evolutionary lives of echinoderm larvae. *Heredity* **97**: 244–252.
- Reitzel, A. M., C. M. Miles, A. Heyland, J. D. Cowart, and L. R. McEdward. 2005. The contribution of the facultative feeding period to echinoid larval development and size at metamorphosis: a comparative approach. *J. Exp. Mar. Biol. Ecol.* **317**: 189–201.
- Sewell, M. A. 2005. Utilization of lipids during early development of the sea urchin *Evechinus chloroticus*. *Mar. Ecol. Prog. Ser.* **304**: 133–142.
- Sewell, M. A., and D. T. Manahan. 2001. Echinoderm eggs: biochemistry and larval biology. Pp. 55–58 in *Echinoderms 2000*, M. Barker, ed. Swets & Zeitlinger, Lisse.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499–506.
- Staver, J. M., and R. R. Strathmann. 2002. Evolution of fast development of planktonic embryos to early swimming. *Biol. Bull.* **203**: 58–69.
- Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annu. Rev. Ecol. Evol. Syst.* **16**: 339–361.
- Strathmann, R. R., J. M. Staver, and J. R. Hoffman. 2002. Risk and the evolution of cell-cycle durations of embryos. *Evolution* **56**: 708–720.
- Thomas, F. I. M., T. F. Bolton, and A. M. Sastry. 2001. Mechanical forces imposed on echinoid eggs during spawning: mitigation of forces by fibrous networks within egg extracellular layers. *J. Exp. Biol.* **204**: 815–821.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**: 1–45.
- Vance, R. R. 1973. On reproductive strategies in marine benthic invertebrates. *Am. Nat.* **107**: 339–352.
- Whitehill, E. A. G., and A. L. Moran. 2012. Comparative larval energetics of an ophiuroid and an echinoid echinoderm. *Invertebr. Biol.* **131**: 345–354.

## Appendix

### Egg volumes and energies for 38 species of echinoderms

Source, species name, collection localities, egg volume, egg biochemical composition, egg energy, and egg energy density of echinoderm species published since McEdward and Morgan's (2001) review. Of these species 29 were not represented in McEdward and Morgan (2001), and of these 29, 5 are species for which samples were collected and analyzed by the authors and are published here for the first time. When data for particular species were published by more than one source, we averaged the values for volume and egg energy prior to data analysis. These species are indicated by footnotes 1–6. If multiple values were reported for a given species in one study (e.g., comparison among sites), we used the average values. Numbers in parentheses are standard errors and are absent if none were available from the original studies. Energy density values were calculated from the energetic and volume data reported in individual studies. Energy and volume values for Moore and Manahan (2007) were not reported in the text, so we estimated values from their figures using ImageJ. P = planktotrophic, L = lecithotrophic, FP = facultatively planktotrophic. N/M = Not measured.

Study	Species	Location	Egg volume (nl)	Protein (ng)	Lipid (ng)	Carb. (ng)	Energy (mJ)	Energy density (mJ/nl)
This study	<i>Arbacia stellata</i> (P)	E. Pacific, Panama	0.13	23.2 (3.0)	9.1 (0.4)	2.5 (0.2)	1.0	7.7
	<i>Lytechinus variegatus</i> <sup>1</sup> (P)	W. Atlantic, Panama	0.38	46.0 (8.2)	20.1 (0.7)	7.8 (1.5)	2.0	5.4
	<i>Lytechinus williamsi</i> (P)	W. Atlantic, Panama	0.51	42.0 (3.2)	18.0 (1.3)	11.2 (0.2)	1.9	3.7
	<i>Toxopneustes roseus</i> (P)	E. Pacific, Panama	0.60	74.4 (10.8)	12.7 (0.7)	6.9 (0.3)	2.4	4.0
	<i>Triplaneustes ventricosus</i> (P)	W. Atlantic, Panama	0.27	23.0 (2.3)	21.4 (0.4)	4.8 (0.5)	1.5	5.6
McAlister & Moran, 2012	<i>Pentaceraster cumingi</i> (P)	E. Pacific, Panama	1.79	229 (11.0)	57.4 (3.4)	21.4 (0.9)	8.1	4.5
	<i>Diadema antillarum</i> (P)	W. Atlantic, Panama	0.18	19.9 (1.4)	9.8 (1.3)	4.9 (0.8)	1.0	5.3
	<i>Diadema mexicanum</i> (P)	E. Pacific, Panama	0.16	18.5 (1.4)	8.1 (1.3)	4.7 (0.8)	0.8	5.2
	<i>Echinometra lucunter</i> <sup>1</sup> (P)	W. Atlantic, Panama	0.31	35.3 (2.1)	17.1 (1.3)	3.3 (0.6)	1.6	5.0
	<i>Echinometra viridis</i> (P)	W. Atlantic, Panama	0.38	35.8 (2.1)	15.4 (1.3)	3.7 (0.6)	1.5	4.0
	<i>Echinometra vanbrunti</i> (P)	E. Pacific, Panama	0.17	29.9 (2.1)	9.4 (1.3)	4.1 (0.6)	1.2	6.8
	<i>Eucidaris tribuloides</i> (P)	W. Atlantic, Panama	0.43	38.4 (2.8)	19.0 (1.3)	5.3 (0.4)	1.8	4.1
	<i>Eucidaris thouarsi</i> (P)	E. Pacific, Panama	0.40	43.5 (2.4)	18.1 (1.1)	4.1 (0.3)	1.8	4.6

## Appendix (Continued)

Study	Species	Location	Egg volume (nl)	Protein (ng)	Lipid (ng)	Carb. (ng)	Energy (mJ)	Energy density (mJ/nl)
Whitehill & Moran, 2012	<i>Ophiocoma alexandri</i> (P)	E. Pacific, Panama	0.19	40.0 (4.0)	11.1 (0.4)	1.9 (0.1)	1.4	7.4
Poorbagher <i>et al.</i> , 2010a	<i>Pseudechinus huttoni</i> (P)	Doubtful Sound, New Zealand	0.72	61.9 (7.7)	15.2 (1.7)	5.3 (0.8)	2.2	3.0
Poorbagher <i>et al.</i> , 2010b	<i>Sclerasterias mollis</i> (P)	Otago, New Zealand	0.98	10 (1.6)	3.6 (0.5)	1.4 (0.2)	4.0	4.1
Prowse <i>et al.</i> , 2008	<i>Patiriella regularis</i> <sup>2</sup> (P)	Matheson's Bay, New Zealand & Hobart, Tasmania	2.35	317.2	121.5	N/M	12.4	5.3
	<i>Meridiastra mortenseni</i> (P)	Auckland, New Zealand	7.15	889.1	313.8	N/M	33.7	4.7
	<i>Meridiastra oriens</i> (L)	Sydney, NSW Australia	33.30	2359.4	6116.9	N/M	298.2	9.0
	<i>Meridiastra calcar</i> <sup>3</sup> (L)	Sydney, NSW Australia	37.40	3102.5	6598.7	N/M	335.1	9.0
	<i>Meridiastra gunnii</i> (L)	Adelaide, South Australia	41.90	3018.2	8980.4	N/M	427.2	10.2
	<i>Parvulastra exigua</i> <sup>4</sup> (L)	Sydney, NSW Australia	29.60	4900.3	3909.0	N/M	272.0	9.2
Byrne <i>et al.</i> , 2008	<i>Tripneustes gratilla</i> (P)	New South Wales, Australia	0.31	87.3 (2.7)	30.8 (1.0)	N/M	3.3	10.5
Moore & Manahan, 2007	<i>Sterechinus neumayeri</i> <sup>5</sup> (P)	McMurdo Sound, Antarctica	3.00	119.7 (2.8)	117 (2.5)	N/M	7.5	2.5
	<i>Odontaster meridionalis</i> (P)	McMurdo Sound, Antarctica	4.38	311.0 (12.0)	247.8	N/M	17.5	4.0
	<i>Odontaster validus</i> <sup>1,6</sup> (P)	McMurdo Sound, Antarctica	5.13	277.1 (12.7)	267.2	N/M	17.4	3.4
Falkner <i>et al.</i> , 2006	<i>Ophionereis schayeri</i> (L)	Sydney, Australia	7.99	430.0	1276.6 (40.9)	N/M	60.7	7.6
	<i>Ophionereis fasciata</i> (P)	Leigh, New Zealand	0.57	24.0	31.6 (2.8)	N/M	1.8	3.2
Reitzel <i>et al.</i> , 2005	<i>Mellita tenuis</i> (P)	Cedar Key, Florida, USA	0.51	49.0 (0.1)	210.0 (0.3)	7.8 (2.5)	9.6	19.0
	<i>Leodia sexiesperforata</i> (P)	Long Key, Florida, USA	2.2	170.0 (16)	510.0 (15.0)	10.0 (0.7)	24.4	11.0
Miner <i>et al.</i> , 2002	<i>Clypeaster rosaceus</i> <sup>1,7</sup> (FP)	Long Key, Florida, USA	10.77	Not reported separately. Energy measured by dichromate oxidation.			110	10.2
Sewell & Manahan, 2001	<i>Odontaster validus</i> <sup>1,6</sup> (P)	McMurdo Sound, Antarctica	5.52	Not reported separately. Egg volumes and egg energies from M.A. Sewell, pers. comm.			20.5	3.7
	<i>Sterechinus neumayeri</i> <sup>5</sup> (P)	McMurdo Sound, Antarctica	3.38				11.0	3.2
Moreno & Hoegh-Guldberg 1999	<i>Patiriella regularis</i> <sup>2</sup> (P)	Tasmania, Australia	1.77	Energy content estimated by Moreno & Hoegh-Guldberg (1999) from ash free dry weight and predicted ratios of protein, lipid, and carbohydrate from Jaeckle (1995).			14.4	8.1
	<i>Patiriella calcar</i> <sup>3</sup> (L)	Sydney, Australia	37.40				410.0	11.0
	<i>Patiriella exigua</i> <sup>4</sup> (L)	Sydney, Australia	31.10				376.0	12.1
Hoegh-Guldberg & Emlet, 1997	<i>Heliocidaris erythrogramma</i> (L)	Sydney, Australia	30.40	Energy content estimated by Hoegh-Guldberg & Emlet (1997) from ash free dry weight and predicted ratios of protein, lipid, and carbohydrate from Jaeckle (1995).			509.8	16.8
	<i>Heliocidaris tuberculata</i> (P)	Sydney, Australia	0.46				3.4	7.3

<sup>1</sup> For data analyses, table values were averaged with data for the same species given in McEdward & Morgan (2001).<sup>2</sup> Values were averaged for data analyses.<sup>3</sup> Values were averaged for data analyses.<sup>4</sup> Values were averaged for data analyses.<sup>5</sup> Values were averaged for data analyses.<sup>6</sup> Values were averaged for data analyses.<sup>7</sup> For data analyses and graphs, *C. rosaceus* was considered a lecithotroph because (1) larvae do not need to feed to reach metamorphosis, and (2) the energy density of *C. rosaceus* was similar to the average energy density of lecithotrophic species.