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

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 _., 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

and Morgan's (2001) original, smaller dataset. On its face, this result appears to support Jaeckle's (1995) conclusion that "free-spawned echinoderm eggs are proportionately identical, *i.e.*, all characters scale to egg volume"

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 (*Luidia*, *Ophioderma*, and *Strongylocentrotus*). Linear regression (SigmaPlot ver. 12, SysStat Software, Inc.) was used to calculate scaling exponents and goodness of fit ( ) from log-log transformed data (Jaeckle, 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; Jaeckle, 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 (= 0.98) (Fig. 1), identical to the results from the McEdward

ual = −

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

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   64: 149–158.

Brusca, G. J., R. C. Brusca, and S. F. Gilbert. 1997. Characteristics of metazoan development. Pp. 3–19 in   , S. F. Gilbert and A. M. Raunio, eds. Sinauer Associates, Sunderland, MA.

Byrne, M., and A. Cerra. 2000. Lipid dynamics in the embryos of   species (Asteroidea) with divergent modes of development.   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   , 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   155: 473–482.

Emlet, R. B., and O. Hoegh-Guldberg. 1997. Effects of egg size on postlarval performance: experimental evidence from a sea urchin.   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   , M.J. Jangoux and J.M. Lawrence, eds. Balkema, Rotterdam.

Falkner, I., M. Byrne, and M. A. Sewell. 2006. Maternal provisioning in   and   brittle stars with contrasting modes of development.   211: 204–207.

Farley, G. S., and D. R. Levitan. 2001. The role of jelly coats in sperm-egg encounters, fertilization success, and seleciton on egg size in broadcast spawners.   157: 626–636.

Gilbert, S. F. 2006.   , 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   , 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.   13: 112–116.

Hand, C. E., and J. F. Honek. 2005. Biological chemistry of naturally occurring thiols of microbial and marine origin.   68: 293–308.

Hoegh-Guldberg, O., and R. B. Emlet. 1997. Energy use during the development of a lecithotrophic and a planktotrophic echinoid.   192: 27–40.

Jackson, J. B. C., and A. Herrera Cubilia. 2000. Adaptation and constraint as determinants of zooid and ovicell size among encrusting ascophoran cheilostome Bryozoa from opposite sides of the Isthmus of Panama. Pp. 249–258 in   , A. Herrera Cubilia and J. B. C. Jackson, eds. 26–31 January 1998. Tropical Research Institute, Balboa, Panama.

Jaeckle, 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   , 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.   135: 1–13.

Levitan, D. R. 1993. The importance of sperm limitation to the evolution of egg size in marine invertebrates.   141: 517–536.

Levitan, D. R. 1996. Predicting optimal and unique egg sizes in free-spawning marine invertebrates.   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.   156: 175–192.

Levitan, D. R. 2006. The relationship between egg size and fertilization success in broadcast-spawning marine invertebrates.   46: 298–311.

Levitan, D. R., and S. D. Irvine. 2001. Fertilization selection on egg and jelly-coat size in the sand dollar   55: 2479–2483.

Luttikhuizen, P. C., P. J. C. Honkoop, and J. Drent. 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve   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.   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   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.   96: 267–286.

McEdward, L. R. 1996. Experimental manipulation of parental investment in echinoid echinoderms.   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.   200: 33–50.

Mercier, A., M. A. Sewell, and J.-F. Hamel. 2013. Pelagic propagule duration and developmental mode: reassessment of a fading link.   22: 517–530.

Meyer, E., A. J. Green, M. Moore, and D. T. Manahan. 2007. Food availability and physiological state of sea urchin larvae (   ).   152: 179–191.

Miner, B. G., J. D. Cowart, and L. R. McEdward. 2002. Egg energetics for the facultative planktotroph   (Echinodermata: Echinoidea), revisited.   202: 97–99.

Moore, M., and D. T. Manahan. 2007. Variation among females in egg

lipid content and developmental success of echinoderms from Mc-Murdo Sound, Antarctica. _ _ _. **30:** 1245–1252.

Moran, A. L. 2004. Egg size evolution in tropical American arcid bivalves: The comparative method and the fossil record. _ , , **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? _ _ _ **216:** 226–242.

Moreno, G., and O. Hoegh-Guldberg. 1999. The energetics of development of three congeneric seastars (_ , _ Verrill, 1913) with different types of development. _ . _ . _ , _. _ **235:** 1–20.

Mtango, N. R., S. Potireddy, and K. Latham. 2008. Oocyte quality and maternal control of development. , . _ _. _ , _ **268:** 223–290.

Podolsky, R. D. 2001. Evolution of egg target size: an analysis of selection on correlated characters. _ , , **55:** 2470–2478.

Podolsky, R. D. 2004. Life-history consequences of investment in free-spawned eggs and their accessory coats. . . **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. . . **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 _ , _. larvae. . . , _ . **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 _ , , _ larvae (Echinodermata: Echinoidea). . , _ . **6:** 302–314.

Prowse, T. A. A., M. A. Sewell, and M. Byrne. 2008. Fuels for development: evolution of maternal provis88.-mng4-uelsseae-off.

Appendix (_continued_)

Study	Species	Location	Egg volume (nl)	Protein (ng)	Lipid (ng)	Carb. (ng)	Energy (mJ)	Energy density (mJ/nl)
Whitehill & Moran, 2012	(P)	E. Pacific, Panama	0.19	40.0 (4.0)	11.1 (0.4)	1.9 (0.1)	1.4	7.4
Poorbagher _et al.,_ 2010a	(P)	Doubtful Sound, New Zealand	0.72	61.9 (7.7)	15.2 (1.7)	5.3 (0.8)	2.2	3.0
Poorbagher _et al.,_ 2010b	(P)	Otago, New Zealand	0.98	10 (1.6)	3.6 (0.5)	1.4 (0.2)	4.0	4.1
Prowse _et al.,_ 2008								