MSL 612: Early Life Histories of Marine Invertebrates

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Class meeting times: T/Th 2:00 – 3:30
Location: TBA
Office hours: By appointment

Prerequisites: Graduate standing; upper-division undergraduates with permission of instructor. *Recommended:* Invertebrate Zoology or Marine Ecology Field Course

Course Description

This will provide advanced students in marine science with an in-depth look at the reproductive biology of marine invertebrates. We will explore invertebrate reproduction, from the production of eggs and sperm to the successful transformation into the juvenile form, and all steps in between. Throughout this course we will consider environmental constraints on reproduction and larval ecology, and their effects on the evolution of early life-history strategies in the marine environment. The production, movement, and survival of larval forms is a central theme in many current issues in marine ecology, including invasive species, establishment of marine reserves, and impacts of climate change on marine communities. This course thus aims to provide students with a solid understanding of reproductive ecology, and an opportunity to critically examine current research in the field. The course will be structured in a lecture format, but will include regular group discussions of the primary literature.

Learning Objectives

1. Identify typical invertebrate larval forms, become familiar with the classification schemes used to describe larvae, and understand the role of larval forms in defining invertebrate taxonomic relationships.
2. Become familiar with the basic biological processes of gamete production, fertilization, embryogenesis, and larval development in marine invertebrates.
3. Examine the influence of environmental variables on larval development, dispersal and recruitment, and consider the potential effects of these variables on the evolution of marine life-history strategies.
4. Critically evaluate and discuss current research topics in which marine life-history strategies play an important role.
5. Explore current research methods relevant to life-history studies.

Course Policies and Requirements

Check your email regularly, and be sure I have your current contact information throughout the semester. Class information, updates, readings, and changes to the schedule will be distributed via email.

Class participation and active engagement in **group discussions** (including those associated with student presentations—see below) is expected from ALL students. Points for class participation will be applied toward the final grade, as indicated below. Key ideas presented in group discussions can also be expected to appear on exams.

Two **midterms** and one **final exam** will be given during the course. These exams will be written, closed-book, short-answer and/or essay exams, and must be completed during the normal class period. The final exam will include material presented throughout the semester, but will be weighted toward material covered after the midterm.

Homework assignments may be made during the semester. Students are encouraged to collaborate on these assignments where appropriate, but each student will be responsible for submitting his/her own completed assignment at the requested time. Late assignments will not be accepted unless prior approval is obtained from the instructor.

Group Discussions
Plan on discussing as many as two readings from the primary literature during each lecture session at a *maximum*, although we will probably not have time to discuss two readings every class period. Readings will be selected by the instructor, unless otherwise noted, and will be distributed via email a week in advance. All students will be expected to participate in discussions. This process is very important in developing a command of the scientific literature and identifying factors that will make our own writing interesting, effective, and publishable—PLEASE BE PREPARED. When preparing for these sessions, ask yourself the following questions, which we will use as a guide for our discussion:

- Why was this reading assigned? What is the relevance to the lecture topic?
- What is the purpose of the paper? Is the purpose clearly stated? Justified?
- Question/Objective/Hypotheses: Is the question or hypothesis well-stated? Is it relevant to the stated purpose?
- Methods: Are the methods sound? Are they appropriate to the hypothesis stated? What would you do differently? What assumptions are inherent in the methods? Are these assumptions reasonable/acceptable/justified?
- Results: What are the key results? Do they address the stated hypothesis? Was the hypothesis accepted/rejected? Do the figures present the results clearly? Identify figures that are especially useful in conveying the important findings—what do you like about them? What do they tell you?
- Discussion: Do the conclusions follow from the results? Are they presented in a broader context of other work done in the field? Are there broader implications for the field of marine science/biology/fisheries? Are the results relevant in any way to your own work? Are there any major questions suggested by the findings? What would you propose as 'the next step' for this line of research?

• General editorial critique: Was the paper easy to follow? Why or why not? Was there information missing that would have helped clarify any aspect of the study? Did each section of the paper contain the appropriate material? Were the figures clear, useful, and easy to interpret?

Readings

No textbook is required for this course; readings will be assigned from the primary literature. All readings will either be distributed via email, or placed on **eReserves** (http://eres.uaf.edu/eres/default.aspx) **[PASSWORD: larvae]**. In addition to required discussion readings, I will provide a general **review paper or book chapter** for each topic wherever possible. These review papers are listed on the lecture schedule below. A **master reading list** organized by topic will also be distributed to you and updated periodically throughout the semester. This list will contain citations for all references provided to you, those cited in lectures and any additional papers of potential interest. If you have trouble obtaining any of these references from the library, let me know and I will help you to obtain a copy.

PLEASE NOTE: You are young professional scientists, and as such, a command of the current literature in your field is essential, as is an ability to allocate your time in the most effective manner. *I will thus expect you to take responsibility for deciding how and where to spend your time on readings*. Here are a few guidelines:

• Readings from the published scientific literature will be discussed in class, as described above. In preparing exam questions, I WILL assume you are familiar with the general concepts and ideas presented in these readings. I WILL NOT expect you to recall detailed information about, e.g., specific figures, etc.
• Review papers may be used in lieu of a text book. How you use them is up to you. If you feel you need a source of additional background reading on lecture topics, skim the reviews for relevant points. If not, consider them an addition to your personal library.
• I will present results and ideas from the relevant scientific literature in lectures, and will provide citations on the slides wherever appropriate. If I mentioned it in class, that probably means I think it is important, so refer to the master reading list if you missed something or want to take a closer look at an original source mentioned in lecture.

Several useful (but not required) **texts** are listed below. These books will be placed on physical reserve at the UAF BioSci Library for the entire semester. An invertebrate zoology text (e.g., Brusca & Brusca) is recommended and should be in the library of all marine biology students; if you do not already own one, you may want to consider a purchase (used copies can often be found for low prices):

Brusca, R.C. & Brusca, G.J. (2003) Invertebrates. Sinauer & Associates, Inc., Sunderland, MA, 936 pp.
[This quintessential invertebrate zoology text should be in every marine biologist's personal library! Useful chapters include Ch. 4 on reproduction and larval forms.]

McEdward, L. (1995) Ecology of Marine Invertebrate Larvae. CRC Press, Boca Raton, 464 pp. *[A collection of review papers that summarize many of the topics we will cover in this course. Although these papers are several years old, they are still useful as reviews of the "classic" literature.]*

Gilbert, S.F. (2006) Developmental Biology. Sinauer & Associates, Inc., Sunderland, MA, 817 pp. *[A developmental biology text with more detailed information on early embryology, including gene expression, cell communication, and other topics of potential interest.]*

Young, C. M., Sewell, M. A. & Rice, M. E. (2002) Atlas of Marine Invertebrate Larvae. Academic Press, San Diego, 626 pp. *[A beautiful illustrated atlas of larval forms organized by phyla, with good general information about the life-cycle of each group.]*

Student Presentations: An assignment for a presentation will be made in the first week of the course. The specific topics of these presentations will be chosen by the students with guidance from the instructor. Students are expected to present a general introduction to the chosen topic, and are encouraged to relate the topic to their own research. Presentations will be approximately 30 minutes in length. In addition, students will *assign a relevant paper* on the topic presented, and lead a group discussion on the paper per the usual protocol. We will all provide reviews of each student presentation using a standard form that will be distributed in class. Reviews will be collected by the instructor after each presentation and comments provided to the speaker. If you wish for your comments to remain anonymous, please notify the instructor when handing in your review sheet.

A note about plagiarism: Plagiarism will not be tolerated in any way during this course. All assignments are expected to consist of students' original ideas and/or information from *properly cited* published sources. Students may seek assistance with proper referencing of scientific literature from the instructor as needed.

Grading

Grades will be determined based on the absolute points awarded for the following requirements:

	Possible points	% of total
Class participation (attendance, preparedness, etc.)	50	10
Homework assignments	50	10
Midterm1	100	20
Midterm 2	100	20
Presentation	100	20
Final exam	100	20
Total	**500 pts.**	**100%**

Semester grades will be assigned according to the following scale:

A+ 98-100%	A 93-97%	A- 90-92%	
B+ 87-89%	B 83-86%	B- 80-82%	
C+ 77-79%	C 73-76%	C- 70-72%	
D+ 67-69%	D 63-66%	D- 60-62%	F <60%

Support and Disability Services
The Office of Disability Services (203 WHIT; 474-5655; fydso@uaf.edu) implements the Americans with Disabilities Act and insures that UAF students have equal access to the campus and course materials. Students with physical or learning disabilities should contact this office, or the instructor, as soon as possible so that suitable arrangements can be made to accommodate specialized needs.

Lecture Schedule (Subject to change**):**

Week	Date	Lecture Topic	Assignments/Readings
1	9/2	Introductions, Course overview and goals	
2	9/7	Invertebrate zoology review; Classification of life-history modes	Brusca & Brusca Ch. 4; McEdward Ch. 1
	9/9	Embryology review; Generalized larval forms	Nielsen 1998
3	9/14	Origin of complex life cycles: Why are there larvae?	McEdward Ch. 13
	9/16	Diversity of life-history modes	Young et al. 2002 text as needed
4	9/21	Diversity of life-history modes (cont.)	
	9/23	Diversity of life-history modes (cont.)	
5	9/28	**Guest lecture** (Katrin Iken): Reproduction in macroalgae	
	9/30	Evolutionary transitions in life-history modes	McEdward Ch. 3
6	10/5	**Midterm #1**	
	10/7	Evolution of brooding	Strathmann & Strathmann 1982
7	10/12	Egg size models	McEdward Ch. 2
	10/14	Larval mortality and selective pressures	Strathmann 2007; Vaughn & Allen 2010
8	10/19	Fertilization; gamete competition; sexual selection	Levitan 1998; Yund 2000
	10/21	Special topics: Reproduction in the deep-sea	Young 2004
9	10/26	Maternal investment; Gametogenesis and spawning	McEdward Ch. 5; Marshall et al. 2008
	10/28	Larval diet and nutrition	McEdward Ch. 7
10	11/2	Latent effects of larval experience	Pechenik 2006
	11/4	Larval swimming and feeding; Boundary layer processes	Metaxas 2001
11	11/9	**Midterm #2**	
	11/11	Special topics: Ocean acidification effects on larvae	Dupont & Thorndyke 2009

12	11/16	Larval dispersal: Physical processes and population connectivity	
	11/18	Larval dispersal, range size, and population effects	Shanks 2009
13	11/23	**Guest lecture** (Georgina Gibson): Dispersal modeling	
	11/25	Recruitment processes: Larval behavior and habitat selection	Elkin & Marshall 2007
14	11/30	Recruitment and population dynamics	Menge 2000
	12/2	Special topics: Marine protected area design principles	Gaines et al. 2007
15	12/7	Student presentations	
	12/9	Student presentations	
16		**Final exam**	

Recommended Reading List

Assigned readings are in indicated with asterisks (**). The remaining references are suggested supplementary readings that may be of interest, including "classic" papers and citations presented in lectures. *This is a preliminary list that will be updated and revised throughout the semester.*

Useful General Texts

Brusca, R.C. & Brusca, G.J. (2003) *Invertebrates*. Sinauer & Associates, Inc., Sunderland, MA, 936 pp.

Gilbert, S.F. (2006) *Developmental Biology*. Sinauer Associates, Inc., Sunderland, MA, 817 pp.

Nielsen, C. (2001) *Animal Evolution: Interrelationships of the living phyla*. Oxford University Press, Oxford, 563 pp.

Shanks, A.L. (2001) *An identification guide to the larval marine invertebrates of the Pacific Northwest*. Oregon State University Press, Corvallis, OR, 314 pp.

Young, C. M., Sewell, M. A. & Rice, M. E. (2002) *Atlas of Marine Invertebrate Larvae*. Academic Press, San Diego, 626 pp.

Embryology and origins of the metazoa

Chen, J.-Y., Oliveri, P., Li, C.-W., Zhou, G.-Q., Gao, F., Hagadorn, J. W., Peterson, K. J. & Davidson, E. H. (2000) Precambrian animal diversity: Putative phosphatized embryos from the Doushantuo Formation of China. *Proc Nat Acad Sci*, **97**, 4457-4462.

Degnan, S. M. & Degnan, B. M. (2006) The origin of the pelagobenthic metazoan life cycle: what's sex got to do with it? *Integrative & Comparative Biology*, **46**, 683-690.

Marshall, C. R. (2006) Explaining the Cambrian "explosion" of animals. *Annual Review of Earth and Planetary Sciences*, **34**, 355-384.

Nielsen, C. (1994) Larval and adult characters in animal phylogeny. *American Zoologist*, **34**, 492-501.

Nielsen, C. (1998) Origin and evolution of animal life cycles. *Biological Reviews*, **73, 125-155.

Nielsen, C. (2008) Six major steps in animal evolution: are we derived sponge larvae? *Evolution & Development*, **10**, 241-257.

Rieger, R. M. (1994) The biphasic life cycle: A central theme of metazoan evolution. *American Zoologist*, **34**, 484-491.

Sly, B. J., Snoke, M. S. & Raff, R. A. (2003) Who came first--larvae or adults? Origins of bilaterian metazoan larvae. *International Journal of Developmental Biology*, **47**, 623-632.

Diversity and classification of life-history modes

Bishop, C. D., Erezyilmaz, D. F., Flatt, T., Georgiou, C. D., Hadfield, M. G., Heyland, A., Hodin, J., Jacobs, M. W., Maslakova, S. A., Pires, A., Reitzel, A. M., Santagata, S., Tanaka, K. & Youson, J. H. (2006) What is metamorphosis? *Integrative & Comparative Biology*, **46**, 655-661.

Byrne, M. (2006) Life history diversity and evolution in the Asterinidae. *Integrative and Comparative Biology*, **46**, 243-254.

Chia, F. S. (1974) Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugoslavica*, **10**, 121-130.

Galley, E. A., Tyler, P. A., Clarke, A. & Smith, C. R. (2005) Reproductive biology and biochemical composition of the brooding echinoid *Amphipneustes lorioli* on the Antarctic continental shelf. *Marine Biology*, **148**, 59-71.

Gibson, G. D. & Gibson, A. J. F. (2004) Heterochrony and the evolution of poecilogony: Generating larval diversity. *Evolution*, **58, 2704-2717.

Grahame, J. & Branch, G. M. (1985) Reproductive patterns of marine invertebrates. *Oceanography and Marine Biology: an Annual Review*, **23**, 373-398.

Hickman, C. S. (1999) Larvae in invertebrate development and evolution. *The Origin and Evolution of Larval Forms* (ed. by B.K. Hall & M.H. Wake), pp 21-59. Academic Press, San Diego, CA.

** Levin, L. A. & Bridges, T. S. (1995) Pattern and diversity in reproduction and development. *Ecology of Marine Invertebrate Larvae* (ed. by L. McEdward), pp 1-48. CRC Press, Boca Raton, FL.

McEdward, L. R. & Janies, D. A. (1993) Life cycle evolution in Asteroids: What is a larva? *Biological Bulletin*, **184**, 255-268.

McEdward, L. R. (1995) Evolution of pelagic direct development in the starfish *Pteraster tesselatus* (Asteroidea: Velatida). *Biological Journal of the Linnean Society*, **54**, 299-327.

McEdward, L. R. & Miner, B. G. (2001) Larval and life-cycle patterns in echinoderms. *Canadian Journal of Zoology*, **79**, 1125-1170.

Mileikovsky, S. A. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Marine Biology*, **10**: 193-213.

Rouse, G., Wilson, N., Goffredi, S., Johnson, S., Smart, T., Widmer, C., Young, C. & Vrijenhoek, R. (2009) Spawning and development in *Osedax* boneworms (Siboglinidae, Annelida). *Marine Biology*, **156**, 395-405.

Rouse, G. W., Goffredi, S. K. & Vrijenhoek, R. C. (2004) *Osedax*: Bone-eating marine worms with dwarf males. *Science*, **305**, 668-671.

Rouse, G. W., Worsaae, K., Johnson, S. B., Jones, W. J. & Vrijenhoek, R. C. (2008) Acquisition of dwarf male "harems" by recently settled females of *Osedax roseus* n. sp. (Siboglinidae; Annelida). *Biol Bull*, **214**, 67-82.

Strathmann, R. R., Fenaux, L. & Strathmann, M. F. (1992) Heterochronic developmental plasticity in laraval sea urchins and its implications for evolution of nonfeeding larvae. *Evolution*, **46**, 972-986.

Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews of the Cambridge Philosophical Society*, **25**, 1-45.

Evolution of complex life-cycles and larval forms; Selective pressures on life-history modes

Chia, F. S. (1974) Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugoslavica*, **10**, 121-130.

Collin, R., Chaparro, O. R., Winkler, F. & Veliz, D. (2007) Molecular phylogenetic and embryological evidence that feeding larvae have been reacquired in a marine gastropod. *Biol Bull*, **212**, 83-92.

Gillespie, J. M. & Mcclintock, J. B. (2007) Brooding in echinoderms: How can modern experimental techniques add to our historical perspective? *Journal of Experimental Marine Biology and Ecology*, **342**, 191-201.

Havenhand, J. N. (1993) Egg to juvenile period, generation time, and the evolution of larval type in marine invertebrates. *Marine Ecology Progress Series*, **97**, 247-260.

** Havenhand, J. N. (1995) Evolutionary ecology of larval types. *Ecology of Marine Invertebrate Larvae* (ed. by L. Mcedward), pp 78-122. CRC Press, Boca Raton.

Hickman, C. S. (1999) Larvae in invertebrate development and evolution. *The Origin and Evolution of Larval Forms* (ed. by B.K. Hall & M.H. Wake), pp 21-59. Academic Press, San Diego, CA.

Laptikhovsky, V. (2006) Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology*, **27**, 7-14.

McEdward, L. R. (2000) Adaptive evolution of larvae and life cycles. *Seminars in Cell & Developmental Biology*, **11**, 403-409.

Nielsen, C. (2009) How did indirect development with planktotrophic larvae evolve? *Biol Bull*, **216**, 203-215.

Page, L. R. (2009) Molluscan larvae: Pelagic juveniles or slowly metamorphosing larvae? *Biol Bull*, **216**, 216-225.

Pernet, B. (2003) Persistent ancestral feeding structures in nonfeeding annelid larvae. *Biological Bulletin*, **205**, 295-307.
Peterson, K. J. (2005) Macroevolutionary interplay between planktic larvae and benthic predators. *Geology*, **33**, 929-932.
Poulin, E. & Feral, J.-P. (1996) Why are there so many species of brooding Antarctic echinoids? *Evolution*, **50**, 820-830.
Poulin, E., Palma, A. T. & Feral, J.-P. (2002) Evolutionary versus ecological success in Antarctic benthic invertebrates. *Trends in Ecology and Evolution*, **17**, 218-222.
Raff, R. A. (2008) Origins of the other metazoan body plans: the evolution of larval forms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1473-1479.
Rouse, G. W. (2000) Polychaetes have evolved feeding larvae numerous times. *Bulletin of Marine Science*, **67**, 391-409.
Strathmann, R. R. (1978) The evolution and loss of feeding larval stages of marine invertebrates. *Evolution*, **32**, 894-906.
Strathmann, R. R. (1985) Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics*, **16**, 339-361.
Strathmann, R. R. (1990) Why life histories evolve differently in the sea. *American Zoologist*, **30**, 197-207.
Strathmann, R. R. (1993) Hypotheses on the origins of marine larvae. *Annual Review of Ecology and Systematics*, **24**, 89-117.
Strathmann, R. R. (2007) Three functionally distinct kinds of pelagic development. *Bulletin of Marine Science*, **81, 167-179.
Varpe, Ø., Jørgensen, C., Tarling, G. A. & Fiksen, Ø. (2007) Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos*, **116**, 1331-1342.
Villinski, J. T., Villinski, J. C., Byrne, M. & Raff, R. A. (2002) Convergent maternal provisioning and life-history evolution in echinoderms. *Evolution*, **56**, 1764-1775.
** Wray, G. A. (1995) Evolution of larvae and developmental modes. *Ecology of Marine Invertebrate Larvae* (ed. by L. Mcedward), pp 413-447. CRC Press, Boca Raton.
Wray, G. A. (1995) Punctuated evolution of embryos. *Science*, **267**, 1115-1116.

Egg size and maternal investment

Alcorn, N. J. & Allen, J. D. (2009) How do changes in parental investment influence development in echinoid echinoderms? *Evolution & Development*, **11**, 719-727.
Allen, J. D., Zakas, C. & Podolsky, R. D. (2006) Effects of egg size reduction and larval feeding on juvenile quality for a species with facultative-feeding development. *Journal of Experimental Marine Biology and Ecology*, **331**, 186-197.
Allen, Richard M., Buckley, Yvonne M. & Marshall, Dustin J. (2008) Offspring size plasticity in response to intraspecific competition: An adaptive maternal effect across life-history stages. *The American Naturalist*, **171**, 225-237.
Bernardo, J. (1996) Maternal effects in animal ecology. *American Zoologist*, **36**, 83-105.
Bertram, D. F. & Strathmann, R. R. (1998) Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. *Ecology*, **79**, 315-327.
Christiansen, F. B. & Fenchel, T. M. (1979) Evolution of marine invertebrate reproductive patterns. *Theoretical Population Biology*, **16**, 267-282.
Crean, A. J. & Marshall, D. J. (2009) Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **364**, 1087-1096.

Emlet, R. B. & Hoegh-Guldberg, O. (1997) Effects of egg size on postlarval performance: Experimental evidence from a sea urchin. *Evolution*, **51**, 141-152.

Emlet, R. B., McEdward, L. R. & Strathmann, R. R. (1987) Echinoderm larval ecology viewed from the egg. *Echinoderm Studies* (ed. by M. Jangoux & J.M. Lawrence), pp 55-136. A.A. Balkema, Rotterdam.

George, S. B. (1996) Echinoderm egg and larval quality as a function of adult nutritional state. *Oceanologica Acta*, **19**, 297-308.

George, S. B. (1999) Egg quality, larval growth and phenotypic plasticity in a forcipulate seastar. *Journal of Experimental Marine Biology and Ecology*, **237**, 203-224.

** Jaeckle, W. B. (1995) Variation in the size, energy content, and biochemical composition of invertebrate eggs: Correlates to the mode of larval development. *Ecology of Marine Invertebrate Larvae* (ed. by L. McEdward), pp 49-77. CRC Press, Boca Raton.

Laptikhovsky, V. (2006) Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. *Marine Ecology*, **27**, 7-14.

Levitan, D. R. (1996) Predicting optimal and unique egg sizes in free-spawning marine invertebrates. *American Naturalist*, **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. *American Naturalist*, **156**, 175-192.

Marshall, D. J., Bolton, T. F. & Keough, M. J. (2003) Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. *Ecology*, **84**, 3131-3137.

Marshall, D. J. (2008) Transgenerational plasticity in the sea: Context-dependent maternal effects across the life history. *Ecology*, **89**, 418-427.

Marshall, D. J., Allen, R. M. & Crean, A. J. (2008) The ecological and evolutionary importance of maternal effects in the sea. *Oceanography and Marine Biology. An Annual Review*, **46**, 203-250.

McAlister, J. S. (2007) Egg size and the evolution of phenotypic plasticity in larvae of the echinoid genus *Strongylocentrotus*. *Journal of Experimental Marine Biology and Ecology*, **352**, 306-316.

McEdward, L. R. (1997) Reproductive strategies of marine benthic invertebrates revisited: Facultative feeding by planktotrophic larvae. *American Naturalist*, **150**, 48-72.

McEdward, L. R. & Janies, D. A. (1997) Relationships among development, ecology, and morphology in the evolution of Echinoderm larvae and life cycles. *Biological Journal of the Linnean Society*, **60**, 381-400.

McEdward, L. R. & Morgan, K. H. (2001) Interspecific relationships between egg size and the level of parental investment per offspring in echinoderms. *Biol Bull*, **200**, 33-50.

Moran, A. L. & Mcalister, J. S. (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.

Mousseau, T. A. & Fox, C. W. (1998) The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, **13**, 403-407.

Podolsky, R. D. & Mcalister, J. S. (2005) Developmental plasticity in *Macrophiothrix* brittlestars: Are morphologically convergent larvae also convergently plastic? *Biological Bulletin*, **209**, 127-138.

Prowse, T., Sewell, M. & Byrne, M. (2008) Fuels for development: evolution of maternal provisioning in asterinid sea stars. *Marine Biology*, **153**, 337-349.

Reitzel, A. M. & Heyland, A. (2007) Reduction in morphological plasticity in echinoid larvae: Relationship of plasticity with maternal investment and food availability. *Evolutionary Ecology Research*, **9**, 109-121.

Sinervo, B. & McEdward, L. (1988) Developmental consequences of an evolutionary change in egg size: An experimental test. *Evolution*, **42**, 885-899.

Smith, C. C. & Fretwell, S. D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499-506.

Sukhotin, A. A. & Flyachinskaya, L. P. (2009) Aging reduces reproductive success in mussels *Mytilus edulis*. *Mechanisms of Ageing and Development*, **130**, 754-761.

Vance, R. R. (1973) On reproductive strategies in marine benthic invertebrates. *American Naturalist*, **107**, 339-352.

Body size and the cost of brooding

Brante, A., Fernandez, M., Eckerle, L., Mark, F., Pörtner, H.-O. & Arntz, W. (2003) Reproductive investment in the crab *Cancer setosus* along a latitudinal cline: egg production, embryo losses and embryo ventilation. *Marine Ecology Progress Series*, **251**, 221-232.

Cohen, C. S. & Strathmann, R. R. (1996) Embryos at the edge of tolerance: Effects of environment and structure of egg masses on supply of oxygen to embryos. *Biological Bulletin*, **190**, 8-15.

Fernandez, M., Bock, C. & Pörtner, H.-O. (2000) The cost of being a caring mother: the ignored factor in the reproduction of marine invertebrates. *Ecology Letters*, **3**, 487-494.

Fernandez, M., Calderon, R., Cifuentes, M. & Pappalardo, P. (2006) Brooding behaviour and cost of brooding in small body size brachyuran crabs. *Marine Ecology-Progress Series*, **309**, 213-220.

Hess, H. C. (1993) The evolution of parental care in brooding Spirorbid polychaetes: The effect of scaling constraints. *The American Naturalist*, **141**, 577-596.

Moran, A. L. & Woods, H. A. (2007) Oxygen in egg masses: interactive effects of temperature, age, and egg-mass morphology on oxygen supply to embryos. *Journal of Experimental Biology*, **210**, 722-731.

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