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The Effect of Gamete Competition on Levels of Gamete Production in a Marine Invertebrate

Kevin J. Eckelbarger

Principal Investigator; University of Maine, Orono, kevine@maine.edu

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Final Report for Period: 05/1998 - 04/2002**Submitted on:** 07/03/2002**Principal Investigator:** Eckelbarger, Kevin J.**Award ID:** 9730354**Organization:** University of Maine**Title:**
The Effect of Gamete Competition on Levels of Gamete Production in a Marine Invertebrate**Project Participants****Senior Personnel****Name:** Yund, Philip**Worked for more than 160 Hours:** Yes**Contribution to Project:****Post-doc****Name:** Meidel, Susanne**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Developed and implemented field fertilization assays.

Graduate Student**Name:** Phillippi, Aimee**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Assisted with field fertilization assays and developed laboratory protocols to test effects of delayed fertilization on subsequent embryonic development. Supported by combination of grant and university funds.

Undergraduate Student**Name:** Wright, Megan**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Summer undergraduate assistant with lab and field work

Name: Whitford, Sarah**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Summer undergraduate assistant - field and lab.

Name: Blich, James**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Undergraduate assistant, summer and fall

Name: Wapnick, Cheryl**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Assisted with field and laboratory work

Name: Onaga, Lisa**Worked for more than 160 Hours:** Yes**Contribution to Project:**

Assisted with laboratory work and conducted related project on effects of maternal physiological status on gamete production in offspring.

Name: Johnson, Sheri

Worked for more than 160 Hours: Yes

Contribution to Project:

Conducted independent summer project on sperm longevity

Name: Mohamad, Basma

Worked for more than 160 Hours: Yes

Contribution to Project:

Conducted independent summer project on gametic incompatibility

Name: Hamann, Ellen

Worked for more than 160 Hours: Yes

Contribution to Project:

Conducted independent project on effects of population size and density on egg fertilization levels

Name: Choate, Beth Ann

Worked for more than 160 Hours: Yes

Contribution to Project:

Conducted independent project on gametic incompatibility in self vs. out-crossed matings.

Technician, Programmer

Name: Hansen, Rikke

Worked for more than 160 Hours: Yes

Contribution to Project:

Part-time technician, academic year

Other Participant

Research Experience for Undergraduates

Organizational Partners

Other Collaborators or Contacts

John Stewart-Savage, University of New Orleans, conducted experiments on the timing of fertilization (within a reproductive cycle) on fertilization levels, and developed protocols for examining the effects of a possible gametic-compatibility system on fertilization.

Paul Rawson, University of Maine, instructed a grad student (Aimee Phillippi) in the use of PCR to amplify microsatellites for possible use in paternity analysis.

Activities and Findings

Research and Education Activities:

This project addressed the general question of whether fertilization in a free-spawning brooding colonial invertebrate (i.e., one that releases sperm, but broods eggs) is dominated by sperm limitation or sperm competition, and the role that these two processes play in selecting for different life history attributes (especially patterns of energy allocation to egg vs. sperm production in this cyclical hermaphrodite). Specific activities included 1) extensive breeding experiments to establish the narrow-sense heritability (genetic basis) of sperm and egg production, and genetic correlations among different life history traits, 2) field sampling to evaluate spatial and temporal variation in sperm limitation and the population density patterns that drive those processes, and 3) correlative studies of gamete allocation patterns in natural populations that differ in density.

Findings:

The breeding experiments revealed extremely high narrow-sense heritabilities for sperm and egg production and other life history traits for colonies growing in the field under natural conditions (almost 40% of phenotypic variation in sperm and egg production was genetically based). These high narrow-sense heritabilities are comparable to previously published broad-sense heritabilities, and are consistent with the action of spatial and temporal variation in selective pressures in nature (i.e., genetic variation can accumulate when selection does not consistently favor one phenotype). However, in contrast to previously published phenotypic correlations, we found no genetic correlations among different life history traits, leading us to conclude that selection can act independently on different traits, rather than on particular trait combinations.

Spatial and temporal variation in population density was substantial in nature, and repeatable from year to year (Yund and Stires, in press). However, contrary to our predictions, egg fertilization levels were not correlated with population density. In both surveys of natural spawns and experimental manipulations of population density, most eggs (circa 85%) were consistently fertilized across a broad range of population densities (circa 2-200 colonies per sq. m.) and population sizes (Phillippi et al., in prep.). Failure of the remaining 15% of eggs to fertilize is probably not attributable to sperm limitation, but rather to outbreeding depression incurred in our fertilization assays, which circumvented the local genetic structure of natural populations in this typically inbreeding species (Yund and O'Neil, 2000). The only hint of sperm limitation that we were able to detect in natural spawns came at the very end of the summer reproductive season, when fertilization levels still hovered around 85%, but a portion of the eggs were fertilized too late in their period of viability to complete development prior to the resorption of the maternal zoid (Stewart-Savage et al., 2001; zoid resorption occurs on a regular cycle in this organism). These patterns led us to abandon our hypothesis that sperm limitation (mediated via population density) selects for higher levels of egg production, and focus just on the consequences of sperm competition for sperm production levels (an approach also justified by the absence of a genetic correlation between sperm and egg production).

Our predictions were based on an earlier experiment (prior award) that manipulated sperm competition levels and assayed male reproductive success as a function of sperm production levels. Males that produced few sperm could nevertheless fertilize most eggs in their vicinity, and higher levels of sperm production only increased male reproductive success when sperm competitors were present. Consequently, we predicted that colonies from higher density populations, which should be subject to greater sperm competition, would produce more sperm. As predicted, colonies collected from high density populations, but grown in laboratory common garden experiments, consistently produced more sperm than colonies from low density populations. These results are consistent with selection by density-mediated sperm competition on levels of sperm production, but can not exclude potential effects of phenotypic plasticity induced prior to field collection (via chemical signaling). A recent renewal of this project permits us to continue to explore this issue more directly by using genetic markers (microsatellites) to assay the paternity of colonies that differ in sperm production in natural, genetically-structured populations.

A growing debate on the levels of sperm limitation in natural populations (reviewed in Yund, 2000), coupled with the suggestion from other workers that broadcasters (organisms that spawn eggs as well as sperm) might be more sperm limited than brooders, led us to also explore similarities between our brooding focus species and a broadcaster (a sea urchin). We found these two reproductive systems were much more similar than people expected. Due to an extended period of egg viability, coupled with the release of gametes in sticky, viscous fluids that resist dilution, we found that sea urchin eggs can accumulate fertilizations over an extended period, are often fertilized before advecting away from a female (thus functioning much like an egg brooder; Yund and Meidel, in revision), and hence sperm availability during the time-integrated period of egg viability is often quite high (Meidel and Yund, 2001). These results suggest that our basic conclusions about the role of sperm competition vs. sperm limitation may be more broadly applicable than previously thought.

Training and Development:

In practice, activities were divided into a series of sub-projects so that nine undergraduates could work independently on different portions and be integrated into all phases of those sub-projects. A PhD student, a part-time post-doc, and a part-time technician also participated.

This award provided direct (full or partial) support for seven undergraduate participants. NSF funding was used to leverage partial matching support from a local non-profit foundation for 4 of those 7 students. Two other undergraduates (Ellen Hamann, Augustana College, and Beth Ann Choate, Centerville College) were supported with funds from a REU site grant, but their projects were nevertheless closely tied to the goals of this award.

Outreach Activities:

Presentations at biannual open houses at the Darling Center marine lab focused on introducing the public to problems inherent in uniting gametes that have been released into an aqueous medium. Real time demonstrations of fertilization and vitelline envelope elevation in sand dollars (via a video hook-up to a compound microscope) were particularly well received.

Journal Publications

Yund, Philip O., "How severe is sperm limitation in natural populations of marine free-spawners?", *Trends in Ecology and Evolution*, p. 10, vol. 15, (2000). Published

Yund, P.O., and P.G. O'Neil., "Microgeographic genetic differentiation in a colonial ascidian (*Botryllus schlosseri*) population.", *Marine Biology*, p. 583, vol. 137, (2000). Published

Yund, P.O., and A. Stires., "Spatial variation in population dynamics in a colonial ascidian (*Botryllus schlosseri*).", *Marine Biology*, p. , vol. , (). Accepted

Stewart-Savage, J., Phillippi, A., and P.O. Yund., "Delayed fertilization results in embryo mortality in a brooding ascidian.", *Biological Bulletin*, p. 52, vol. 201, (2001). Published

A. Phillippi, E. Hamann, and P.O. Yund, "Absence of population density effects on fertilization in a brooding colonial ascidian.", *Marine Ecology Progress Series*, p. , vol. , (). In preparation for submission

Meidel, S.K., & P.O. Yund, "Egg longevity and time-integrated fertilization in a temperate sea urchin (*Strongylocentrotus droebachiensis*).", *Biological Bulletin*, p. 84, vol. 201, (2001). Published

Yund, P.O., and S.K. Meidel, "Sea urchin spawning in benthic boundary layers: Are eggs fertilized before advecting away from females?", *Limnology and Oceanography*, p. , vol. , (). Submitted

Newlon, A.W., Yund, P.O., and J. Stewart-Savage, "Phenotypic plasticity of male, female, and asexual reproduction in a colonial ascidian, *Botryllus schlosseri*.", *Proc. Roy. Soc. (London)*, p. , vol. , (). Submitted

Books or Other One-time Publications

Stewart-Savage, J., Stires, A., & P.O. Yund., "Environmental effects on the reproductive output of *Botryllus schlosseri*.", (2001). Book, Published

Editor(s): H. Sawada, H. Yokosama, and C.C. Lambert

Collection: *Biology of Ascidiarians*

Bibliography: Pp. 311-314. Springer-Verlag, Tokyo.

Web/Internet Site

URL(s):

<http://www.ume.maine.edu/~marine/yund.htm>

Description:

Describes past results and work currently in progress.

Other Specific Products

Contributions

Contributions within Discipline:

Our work demonstrates that our focal study species is essentially immune to sperm limitation under ecologically-relevant conditions, and that sperm production levels appear to be influenced by sperm competition. These two results portray a marine system dominated by sperm competition, not sperm limitation, and thus similar to most terrestrial systems. Free-spawning brooders that filter dilute sperm out of the water column may be relatively insensitive to the gamete dilution effects expected in marine systems. Our preliminary work on an egg broadcaster further suggests that some of these organisms may be far less sperm limited than previously suggested, because the combined effects of gamete longevity and viscosity make them function much like egg brooders.

Contributions to Other Disciplines:

Contrary to conventional expectations, fertilization levels in this species did not vary with population density, even at the lowest densities we

could locate in nature. Because fertilization failure at low population density (a form of the Allee effect) is widely anticipated in free-spawning marine species, this result has implications for our understanding of population dynamics in marine systems. Furthermore, many current models of commercially harvested marine species assume fertilization failure at low population density (on the basis of little evidence), so this result casts doubt on a major assumption of some recent fisheries models.

Contributions to Human Resource Development:

Eight out of the nine undergraduates are either continuing their education or working in science or science-related disciplines (e.g., one is a science writer for the journal *Nature*). Two (Johnson, Wapnick) are pursuing their masters degrees; one in Yund's lab, and one at Dauphin Island. Another (Hamann) is a co-author on a manuscript, and an undergrad (Stires) supported on an earlier award (of which this is a renewal) is now co-author on two papers completed under this award. The technician (Hansen) is now enrolled in a PhD program in her native Denmark, and the post-doc (Meidel) is employed by a state environmental agency. A local high school student (not listed in the personnel section) assisted with fertilization experiments on a volunteer basis, and subsequently enrolled in a BS marine biology program at the University of Maine.

Contributions to Resources for Research and Education:

This project provided little enhancement to infrastructure beyond the acquisition of a few pieces of equipment for Yund's lab.

Contributions Beyond Science and Engineering:

The fisheries implications (per earlier section) have societal ramifications, because they support the assumption that population growth in some marine systems will be high at low population densities (i.e., are consistent with one of the most basic tenets of sustainable resource management; that yields increase with harvest).

Categories for which nothing is reported:

Organizational Partners

Any Product