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Internal fertilization and sperm storage in cnidarians: a response to Orr and Brennan

Antonio Carlos Marques^{1,2}, Jimena García¹, and Cheryl Lewis Ames^{3,4}

¹ Institute of Biosciences and Center for Marine Biology, University of São Paulo, R. Matão Tr. 14, 101, 05508-090, São Paulo, Brazil

² Center for Marine Biology, University of São Paulo, Manoel Hypólito do Rego, km. 131,5, 11600-000, São Paulo, Brazil

³ Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20013-7012, USA

⁴ BEES Concentration, Biological Sciences Graduate Program, University of Maryland, College Park, MD 20742, USA

Orr and Brennan [1] recently presented a synthesis of the diversity of sperm storage structures used in internal fertilization in animal taxa and speculated on the selective processes shaping their evolution. Orr and Brennan restrict their discussion of animals with internal fertilization and some type of sperm storage to terrestrial and marine or freshwater benthic and/or nektonic habitats, although they acknowledged that some ctenophores have internal fertilization (see Box 2 in [1]). While we acknowledge that such restrictions are necessary in a short article, we would like to draw attention to a remarkable example that broadens the discussion of ecological and evolutionary variables connected to adaptation in an interesting and informative way. Here, we supplement Orr and Brennan's work [1] with information on internal fertilization and sperm storage structures in basal, planktonic cnidarians.

Planktonic organisms exhibit low probability for random fertilization. The likelihood of success during external fertilization increases with higher numbers of gametes, synchronous spawning, and dense populations (generally the result of extensive asexual reproduction); all variables demand high energetic costs for the fertilization process. However, basal animals, such as medusozoan cnidarians (i.e., jellyfish) in which plesiomorphic external fertilization would be expected in adult medusae [2], offer several interesting examples of disparate jellyfish species exhibiting internal fertilization. The reduction of the sexual medusa to gonophores that remain attached to benthic polyps is a common strategy found in many phylogenetically distantly related hydrozoan clades [3]. Internal fertilization and larval brooding have also been documented in many scyphozoans [4].

But no other early diverging lineage rivals the complexity of sexual reproductive behavior attained in certain cubozoans (i.e., venomous box jellyfish). While their plesiomorphic reproductive mode is external fertilization (e.g., in *Chironex fleckeri*) [5], there is evidence for an evolutionary transformation to the derived strategy of internal fertilization [6]. Cubozoan species such as the carybdeid *Carybdea marsupialis* and the alatinid *Alatina alata* are ovoviviparous, a reproductive mode in which ova

are internally fertilized by sperm taken up by the female medusae during spawning aggregations with males [7].

At the climax of complex cubozoan sexual reproduction is the elaborate behavior seen only in species of Tripedaliidae – *Copula sivickisi* and *Tripedalia cystophora*. These tiny box jellyfish display sexual dimorphism and courtship behavior in which spermatophores are formed by coalescing sperm packets ejaculated from 'seminal receptacles' of the male testes (called hemigonads) [8–11]. Testes are depleted with successive ejaculations during breeding experiments, becoming visibly paler, but sperm content is replenished the next day for subsequent copulations. During pair formation the male uses his tentacles to control the female (Figure 1), bringing her in close to transfer the spermatophore that she invariably ingests (Figure 2). The sperm bundle is accommodated into her gastrovascular cavity (within several hours), which connects the stomach and specialized structures reported to function in sperm storage [8,9,11]. In *C. sivickisi* both polyandry and polygyny are pervasive [8], suggesting sperm competition and opportunities for postcopulatory female choice. Sperm is pigmented (orange or red)



Figure 1. *Copula sivickisi* female (bottom) during pair formation, inducing spermatophore ejaculation – visible as opaque central strands inside male (top). A spermatophore from a previous mate is visible as an orange bundle in the center of the female's stomach. Scale bar: 2 mm. (Image courtesy of Alvaro E. Migotto.)

Corresponding author: Marques, A.C. (marques@ib.usp.br).

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Figure 2. *Copula sivickisi* female (left) inserting spermatophore into her manubrium using her tentacles as the male (right) releases her from his tentacle grip. Scale bar: 2 mm. (Image courtesy of Alvaro E. Migotto.)

(Figure 1) providing an observable cue when sperm disperses from the stomach into the gastrovascular cavity, facilitating internal fertilization within hours to days, after which time the female deposits an embryo strand (unique among cnidarians) onto the substrate [8,10]. One documented change induced by copulation in *C. sivickisi* is the presence of conspicuously dark pigmented velarial spots in sexually active females, which are absent in juvenile females and all males [8]. Histological sectioning of female ovaries in *C. sivickisi* reveals a development gradient [8], and the fact that females accept sperm from males during gestation and after giving birth (i.e., embryo strand release) suggests they might store sperm from multiple copulations for delayed fertilization.

The sperm storage index for *C. sivickisi*, following Orr and Brennan [1], is estimated to be 3, exceeding estimates for sharks, earthworms, and even marsupial mammals (see Box 4 in [1]). It is clear that selective pressures to attain highly specialized internal fertilization (and corresponding sperm storage structures) resulted in several different and sometimes homoplastic strategies in ani-

mals. However, we believe that it is important to emphasize that in the case of tripedalid box jellyfish, selective pressures must have acted on both males and females (i.e., coevolution between the sexes in relation to sperm storage) to enhance fertilization efficiency. This is best put into perspective when recognizing that these morphologically rather simple basal animals inhabit the planktonic realm – a habitat in which organisms are driven by the currents, and, by definition, have incipient or no swimming capacity, drifting almost randomly with little control over mate choice. To increase our understanding of the evolutionary diversity of sperm storage adaptations, we must examine sexual selection in male and female medusozoans from a combined ecological, phylogenetic, and physiological perspective.

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Sperm storage across multiple scales – a reply to Marques, García, and Ames

Teri J. Orr and Patricia L.R. Brennan

Departments of Psychology and Biology, and Organismic and Evolutionary Biology Graduate Program, University of Massachusetts, Amherst, MA 01003, USA

For internally-fertilizing animals, sperm storage is a nearly ubiquitous trait that has enormous evolutionary impli-

Corresponding author: Orr, T.J. (tjorr@cns.umass.edu).

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cations. Female sperm storage (FSS) may influence the degree of pre- and post-copulatory sexual selection as well as the ability of females to time reproduction with periods of resource availability, thereby ensuring an ample supply of sperm when encountering males is unpredictable. In our recent opinion article [1] we developed a framework for studying FSS in a comparative way both by suggesting