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## Review

## Sperm motility of externally fertilizing fish and amphibians

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## ABSTRACT

We review the phylogeny, sperm competition, morphology, physiology, and fertilization environments of the sperm of externally fertilizing fish and amphibians. Increased sperm competition in both fish and anurans generally increases sperm numbers, sperm length, and energy reserves. The difference between the internal osmolarity and iconicity of sperm cells and those of the aquatic medium control the activation, longevity, and velocity of sperm motility. Hypo-osmolarity of the aquatic medium activates the motility of freshwater fish and amphibian sperm and hyperosmolarity activates the motility of marine fish sperm. The average longevity of the motility of marine fish sperm (~550 seconds) was significantly ( $P < 0.05$ ) greater than that of freshwater fish sperm (~150 seconds), with the longevities of both marine and freshwater fish being significantly ( $P < 0.05$ ) lower than that of anuran sperm (~4100 seconds). The average velocity of anuran sperm (25  $\mu\text{m/s}$ ) was significantly ( $P < 0.05$ ) lower than that of marine fish (140  $\mu\text{m/s}$ ) or freshwater fish (135  $\mu\text{m/s}$ ) sperm. The longevity of the sperm of giant salamanders (Cryptobranchioidea) of approximately 600 seconds was greater than that of freshwater fish sperm but much lower than anuran sperm. Our research and information from the literature showed that higher osmolarities promote greater longevity in anuran sperm, and some freshwater fish sperm, and that anuran and cryptobranchid sperm maintained membrane integrity long after the cessation of motility, demonstrating a preferential sharing of energy reserves toward the maintenance of membrane integrity. The maintenance of the membrane integrity of anuran sperm in fresh water for up to 6 hours showed an extremely high osmotic tolerance relative to fish sperm. The very high longevity and osmotic tolerance of anuran sperm and high longevity of cryptobranchid sperm, relative to those of freshwater fish, may reflect the complex fertilization history of amphibian sperm in general and anurans reversion from internal to external fertilization. Our findings provide a greater understanding of the reproductive biology of externally

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## 1. Introduction

The development of reproduction technologies for the sustainable management of fish and amphibians requires knowledge of the factors affecting sperm motility, including sperm phylogeny, competition, morphology, physiology, and fertilization environment. Reproduction technologies are increasingly used for the production of fish and amphibians for food, display, research, and to maintain biodiversity through conservation breeding programs (for fish [1–5]; for amphibians [6–8]). A commonly used reproduction technology for fish [4] and amphibians [7–12] is artificial fertilization through the use of either fresh, refrigerated, or cryopreserved sperm.

Sperm can be harvested by stripping the milt of mature fish [4] or semen of cryptobranchid salamanders [13], and through the hormonal induction [14] of spermic urine or through testes maceration with anurans (frogs and toads [10]). The use of sperm for artificial fertilization greatly reduces the numbers of required male broodstock and increases benefit to cost and reliability in conservation breeding programs, and particularly through cryopreservation enables the perpetuation of genetic variation and therefore biodiversity [7,8]. Consequently, a greater understanding of the mechanisms affecting the motility of fish [15] and amphibian sperm [7,8,11] has considerable potential to provide for the sustainable management of these taxa.

Herein, we have reviewed the physiology and morphology of the sperm of externally fertilizing fish and amphibians and their relationship to activation, sperm competition, swimming modes, metabolism, longevity, and membrane integrity. To provide a stronger empirical foundation for this review, we collated data on the longevity and velocity of the motility in marine and freshwater fish, and amphibians, and the osmolarity of the aquatic medium through a literature search from 1925 to 2012 (Supplementary Tables 1–6), and through correspondence with researchers. In addition, we also review the physiology and morphology of externally fertilizing fish and amphibians with respect to their phylogeny and their evolutionary and current fertilization environments.

Many publications described the relationships between different environmental factors and the longevity and velocity of fish sperm [15–19]. However, there were few similar publications on amphibian sperm [20–23]. To fill research gaps, we held anuran sperm in various osmolarities and assessed their percentage motility and membrane integrity over time.

Data were analyzed to assess the mean longevity and velocity of sperm motility for marine fish, freshwater fish, and anurans. Additionally, we determined and compared the maximum travel distance of sperm from sperm velocity and longevity for each of these groups.

## 2. Phylogeny and fertilization environment

The conceptual framework for understanding the motility of fish and amphibian sperm includes knowledge of their ancestral traits (fish and amphibians [24–27]), recently derived traits (fish [18,19,28,29], amphibians [20–23]), and how these traits relate to the transition from their ancestral to their current fertilization environments.

The earliest fish (placoderms; 416–359 million years ago [mya]) internally fertilized with their decedents the bony fish (teleosts; 409 mya–present) then adopting external fertilization [30]. Sperm morphology shows that the ancestors of amphibians (Lissamphibians, 360 mya) were internal fertilizers as were the earliest amphibian clade, the caecilians, that branched in the Late Carboniferous approximately 340 mya (Fig. 1). The alternate branch, the Batrachians, adopting external fertilization (Fig. 1 [25,26,31]) and then branched into the early internally fertilizing Anura (frogs and toads) and early externally fertilizing Caudata (salamanders and newts) in the Early Permian approximately 300 mya [32,33]. From the Caudata, two fully aquatic and external fertilizing clades independently diverged, the Cryptobranchoidea approximately 220 mya and the Sirenidae 170 mya [33–35; review, see 36], with traditional phylogenetics considering caecilians as included in the Batrachians.

Fertilization modes in amphibians are labile between and within orders (Fig. 1). Derived internal fertilization is present in the majority of Caudata and all Caecilians. Caecilians store sperm in the oviduct [37], and in the Caudate suborder Salamandroidea, which includes most salamanders, sperm is stored in specialized, recently evolved cloacal glands called spermatheca [27]. One member of the fully aquatic Caudate family, the Sirenidae, is also externally fertilizing [38]. Early anurans were internal fertilizers and one anuran (*Ascaphus*) still possesses an intromittent organ for internal fertilization [31]. However, most anurans now fertilize externally, with some having derived internal fertilization with sperm deposition by cloacal apposition [26,31,39]. Sperm morphology can also vary widely between orders, classes, and even families; for instance the ultrastructure of externally fertilizing Cryptobranchoidea (the families Cryptobranchidae and Hynobiidae) sperm makes them distinct from other Caudata on the basis of two synapomorphic characteristics: (1) Absence of mitochondria in the tail and (2) cylindrical shape of the tail axial rod [27].

## 3. Sperm competition and fertilization

To fertilize, sperm must be deposited close to oocytes, compete to be first to locate an oocyte, infiltrate the gel layer of anurans or the chorion of fish, and, in fish, locate and penetrate the micropyle. Externally fertilizing fish and many anurans release sperm into the aquatic environment

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