



Energetics of fish spermatozoa: The proven and the possible



Borys Dzyuba, Olga Bondarenko, Pavel Fedorov, Ievgeniia Gazo, Galina Prokopchuk, Jacky Cosson *

Faculty of Fisheries and Protection of Waters, Research Institute of Fish Culture and Hydrobiology, University of South Bohemia in České Budějovice, Zátěží 728/II, 389 25, Vodnany, Czech Republic

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ABSTRACT

Main features specific to sperm of fish with external fertilization are 1—the seminal fluid osmolality, and in several species, some ions prevent sperm motility in the genital track; 2—transfer from seminal fluid into sea- or freshwater triggers full motility due to osmotic and/or ionic signal; 3—immediately after activation, fish sperm swim with very high efficiency; 4—the motility period is limited to a very short duration for freshwater sperm and not for much longer in case of marine fish spermatozoa; 5—most motility parameters are decreasing and wave shape is changing during the motility period; 6—the regulation of axonemal motility by ionic concentration, as well as by ATP concentration and other substances, can be observed *in vitro* by using membrane-deprived spermatozoa; 7—the chemical energy available in fish spermatozoa is rapidly exhausted during the swimming period; 8—the membrane potential of the spermatozoon represents an important aspect of the cell electro-chemical energy homeostasis; 9—the ultimate task for sperm, before fertilization, is to meet an egg, and this task is facilitated by chemotaxis.

The present chapter will tentatively deal with some of these salient features such as a—osmolality and ionic signals controlling fast but short-lasting motility in connection with ATP and other energetic compounds management; b—role of sperm electro-chemical potential in the *trans*-membrane management of this complementary aspect of sperm energetics; c—considerations on physical energy needed by moving fish flagella; and finally, d—how oriented motility governs sperm behavior while swimming toward egg. Finally, recent studies on applied aspects of fish sperm bioenergetics are summarized.

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1. Introduction

Fish spermatozoa are simple “aquasperm” consisting of a head that is composed of a nucleus and a motility device, called flagellum, and are quite similar to that of sea urchin, a classical model from which most understanding of flagellar beating arises. The ultra-structure of sperm flagella is simple: mostly a scaffold of 9 + 2 microtubules strung with molecular motors—dynein ATPases, which are in charge of generating mechano-chemical forces. The biochemical composition of fish sperm flagella is nevertheless complicated: there are more than 500 regulatory protein components used by flagellum for its operation.

Fish males during spawning deliver sperm in surrounding water at the same time as female's ova. In most fish species, these minute

unicells have to reach the egg micropyle within a very brief period (seconds to minutes), meaning that their highly efficient flagellum must become fully activated immediately on contact with water and propel the sperm cell at a very high initial velocity. The cost of this “hyperactivity” is a very rapid consumption of intracellular energy accumulated as energy of macroergic phosphates (ATP, ADP, and CrP), which outstrips the supply. It is important to recall that ATP hydrolysis is the only source for flagella mechanical motion that is why ADP and CrP should be converted into ATP for utilization of stored energy. The spermatozoa become quickly exhausted since mitochondria cannot compensate for such fast flagellar energy consumption, with the result that spermatozoa cease moving. Within this brief period following activation, various successive events occur from full motility until complete arrest of flagellar activity.

Elucidation of interrelationship between the sperm bioenergetics processes and flagellum mechanical motion leading to successive gamete fusion, even being previously intensively studied, nowadays is still needed. In this chapter, we are updating previously reviewed knowledge with recent data in the field following summary of recent investigation of fish sperm bioenergetics in relation to fish reproduction studies.

Abbreviations: AK, Adenylate kinase; ADP, Adenosine di-phosphate; AMP, Adenosine mono-phosphate; AQP, Aquaporin; ATP, Adenosine tri-phosphate; cAMP, Cyclic-adenosine mono-phosphate; CK, Creatine phospho-kinase; CrP, Creatine-phosphate; GTP, Guanosine tri-phosphate; HSAPs, Herring sperm activating peptides; ROS, Reactive oxygen species; SMIF, Sperm motility initiating factor; TRPs, Transient receptor potential channels.

* Corresponding author.

E-mail address: jacosson@gmail.com (J. Cosson).

2. Chemical energy sources for fish sperm motility

2.1. ATP and other phosphate chemicals as basic energetic compounds

Spermatozoa of most fish species with external fertilization are maintained immotile in the genital ducts, due to the osmolality and ionic composition of the seminal fluid, but initiate motility immediately after dispersion into water environment (Morisawa and Suzuki, 1980). Just after release, spermatozoa need energy to launch and sustain flagellar activity, which is responsible for sperm propulsion. The major role in the motile spermatozoa bioenergetics is assigned to adenylate- and creatine-phosphate metabolisms. Flagella mechanical movement is energetically supported exclusively by dynein ATPase activity. Nevertheless, during motility, ATP level in flagella can be regenerated from ADP by the AK activity or from CrP via CK activity (for review, see Cosson, 2013; Inaba, 2008). Metabolic pathways involved in processes of ATP generation occurring outside of the flagellum, its transport along flagellum, and regeneration near the sites of consumption were comprehensively reviewed by Ingermann (2008) and, until recently, this book chapter could be considered as a description of modern paradigm of fish sperm bioenergetics. From that review, it is clear that ATP level alone is not sufficient as a sole descriptor of the bioenergetic state of spermatozoa and that other metabolites (ADP, CrP) as determinants of motility should be studied. Until recently, just a few studies have been performed in simultaneous quantification of macroergic phosphates pool in relation to fish sperm physiology (Table 1). From data summarized in Table 1, it is clear that species specificity of sperm metabolic pathway do not allow an elaboration of common general rules on description of sperm bioenergetics based on macroergic phosphates content even if the energy consuming process of sperm motility is considered (see Dreanno et al., 1999b; Lahnsteiner and Caberlotto, 2012). Recently, the macroergic phosphates content as a biomarker for semen quality was proposed by several authors (Cabrita et al., 2009; Cabrita et al., 2014; Hatf et al., 2013). However, quite probably this parameter could be used as a marker of sperm quality, only in cases when general species-specific description of macroergic phosphates content is performed. Otherwise, there is a risk of incorrect recognition of the cause of sperm impairment as was shown in striped bass *Morone saxatilis* sperm by Guthrie et al. (2011).

It is important to mention that for comparative studies performed in different laboratories and on different species, the uniformity in data presentation (e.g. content of metabolites) should adopt a same unit, such as mole per number of spermatozoa.

Remark: in column “conditions,” B means before motility activation and A means after motility stop.

Another adenosyl compound, cAMP, was shown to play an important role at motility initiation of fish spermatozoa (Morisawa, 1985), even though it is not directly involved in the generation of energy used by flagellar mechanics (Saudrais et al., 1998) but rather through protein phosphorylation signaling (see Zilli et al., chapter in this book). Nevertheless, cAMP also controls the flagellar activity during the motility period because it has been shown to be strongly interactive with ATP itself (Cosson et al., 1995).

One important point relates to the diffusion rate of energetic compounds along the restricted internal volume of a flagellum. Studies by Takao and Kamimura show that diffusion is a rate-limiting factor for small molecules as predicted in Fig. 1 (Takao and Kamimura, 2008), even though the head-tail junction does not represent a major bottleneck for such diffusion (Takao and Kamimura, 2010). The respective roles of ATP and ADP in the energetic/regulation of flagellar beating are far from being fully understood. Results from a series of studies by Shingyoji's group (see synthesis in Shingyoji, 2009) on sea urchin flagella lead to the unexpected hypothesis that relatively high ATP concentration (above 0.1 mM) partly inhibits the dynein ATPase activity, but this inhibition can be overcome when ADP is present at quite high concentrations. These results indicate that in addition to its role as the source of chemical energy, the physiological concentration of ATP plays a role as an inhibitory factor to prevent dynein arms from causing microtubule sliding, probably by maintaining cross-bridges between certain dynein arms and microtubules. These aspects deserve careful investigation in fish spermatozoa, where the concentrations of both ATP and ADP are subjected to important changes during the motility period.

2.2. Short motility duration of fish spermatozoa

Generally, sperm motility duration in fish is much shorter in comparison to that in mammals and differs greatly among fish species: this suggests that ATP can be generated and stored according to

Table 1
Creatine-phosphate and adenylate-phosphates content in fish sperm before and after motility activation.

Species	ATP	ADP	AMP	CrP	Conditions	References
Siberian sturgeon <i>Acipenser baerii</i>	7.6 nmol per 10 ⁸ spermatozoa				B	Billard et al. (1999)
	4.0 nmol per 10 ⁸ spermatozoa				A	
Turbot <i>Psetta maxima</i>	≈24 nmol per 10 ⁸ spermatozoa	1.4 nmol per 10 ⁸ spermatozoa	0.6 nmol per 10 ⁸ spermatozoa		B	Dreanno et al. (1999b)
	≈6 nmol per 10 ⁸ spermatozoa	8 nmol per 10 ⁸ spermatozoa	6.0 nmol per 10 ⁸ spermatozoa		A	
Turbot <i>Psetta maxima</i>	15.4 nmol per 10 ⁸ spermatozoa	9.9 nmol per 10 ⁸ spermatozoa		72.7 nmol per 10 ⁸ spermatozoa	B	Dreanno et al. (2000)
Sterlet <i>Acipenser ruthenus</i>	5.7 nmol per 10 ⁸ spermatozoa	1.3 nmol per 10 ⁸ spermatozoa		0.7 nmol per 10 ⁸ spermatozoa	B	Fedorov et al. (2015)
	4.5 nmol per 10 ⁸ spermatozoa	1.7 nmol per 10 ⁸ spermatozoa		0.15 nmol per 10 ⁸ spermatozoa	A	
Sea bass <i>Dicentrarchus labrax</i>	11.49 nmol per 10 ⁸ spermatozoa	1.08 nmol per 10 ⁸ spermatozoa	0.57 nmol per 10 ⁸ spermatozoa		B	Dreanno et al. (1999c)
	3.04 nmol per 10 ⁸ spermatozoa	4.03 nmol per 10 ⁸ spermatozoa	8.03 nmol per 10 ⁸ spermatozoa		A	
Common carp <i>Cyprinus carpio</i>	1.29 ± 0.09 nmol/1 μl dry semen	0.058 ± 0.019 nmol/1 μl dry semen	0.024 ± 0.012 nmol/1 μl dry semen	9.64 ± 0.72 nmol/1 μl dry semen	B	Zietara et al. (2009)
African catfish <i>Clarias gariepinus</i>	0.64 ± 0.09 nmol/1 μl dry semen	0.052 ± 0.012 nmol/1 μl dry semen	0.020 ± 0.005 nmol/1 μl dry semen	8.45 ± 0.49 nmol/1 μl dry semen	B	
Gilthead seabream <i>Sparus aurata</i>	16.28 ± 1.35 μmole per ml			26.94 ± 3.28 μmole per ml	B	Lahnsteiner and Caberlotto, (2012)
	20.46 ± 3.77 μmole per ml			32.14 ± 2.21 μmole per ml	A (40% motile cells)	

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