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REVIEW ARTICLE

A Systematic Review of Sperm Competition in Fish Under Biological and Ecohydrological Influence

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ABSTRACT

This review aimed to examine the influence of biological and ecohydrological factors on fish sperm during competition and fertilization to offer a future research framework on fish sperm biology under severe ecological perturbation. Following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines, research on fish sperm biology were retrieved from the Scopus database, Web of Science, Google Scholar, African Journals Online, Data Citation Index, MEDLINE, Science4Life, ScienceDirect and JSTOR. The search criteria focused on peer-reviewed publications from 2000 to 2024 on sperm competition and reproductive biology in Teleostei and Chondrichthyes. From the screening, a total of 177 articles were extracted and included in this study. Among ecohydrological variables, environmental temperature remains the primary factor influencing sperm viability and fertilization success across different fish taxa. Different ion concentration levels: potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}) and pH are required for sperm activation and motility across various environmental media. Theoretical and empirical evidence from various studies indicated that the relationship between sperm competition and reproductive success is complex, often nonlinear, and does not follow a consistent pattern across different fish species. This underscores the need for species-specific research on fish sperm biology and how ecohydrological factors affect sperm performance. Understanding these variables is increasingly important for modelling and predicting fish reproductive outcomes under pollution and environmental stress. Finally, integrating fish sperm physiology and biochemical analysis into ecological risk assessments is important for enhanced conservation strategies, particularly in aquatic ecosystems impacted by climate change, eutrophication, habitat fragmentation, and anthropogenic stress.

Keywords: Ecohydrology; Reproductive physiology; Sperm heteromorphism; Reproductive strategy; Gamete motility; Fish fertilization.

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1.0 INTRODUCTION

Generally, only a single spermatozoon is typically required to fertilize an egg. However, the striking disparity between the number of eggs produced by female organisms and the vast quantity of sperm produced by male organisms has raised fundamental questions among evolutionary biologists. "Why do male organisms invest a large amount of energy in the production of millions of spermatozoa? Addressing this question prompted a thorough understanding of sperm competition as an evolutionary force with profound implications for male reproductive biology (Kowalski & Cejko, 2019). Sperm competition is an evolutionary process whereby spermatozoa from rival males compete to fertilize a set of ova from the female (Parker, 2021). This pre- and post-copulatory sexual selection force exerts substantial influence on the evolution of male reproductive traits such as testis size, sperm morphology, ejaculate composition, and mating behaviours (Ramm et al., 2014; Kowalski & Cejko, 2019; Parker, 2021). These adaptations enhance individual male mating and fertilization success, especially when multiple males compete to fertilize the same female ova. Among ichthyofaunal species, sperm competition is not only widespread but also highly variable, reflecting responses to diverse reproductive modes and ecological pressures (Birkhead et al., 2009; Kowalski & Cejko, 2019). This evolutionary pressure maintains and enhances traits that allow reproductive advantages (increased sperm quantity, faster spermatozoa, or specific behavioural strategies that improve fertilization success). Such traits, which are subject to sexual selection and may be inherited by subsequent generations, shape the reproductive biology of species over evolutionary timescales (Steven et al., 2015; Parker, 2021). A deeper understanding of sperm competition offers a valuable framework for interpreting the evolution of spermatogenesis and its broader role in shaping male reproductive success. This perspective integrates developmental biology, evolutionary theory, and ecological context, reflecting how reproductive traits are optimized under selective pressures of both natural and sexual selection. Sperm competition, a key post-mating sexual selection mechanism, occurs in both internally and externally fertilizing fish and significantly influences paternity outcomes (Parker, 2021) and allows evolutionary differences among male fish to enhance fertilization success and genetic diversity (Poiani, 2006; Parker, 2014; Sirot et al., 2015). However, competition among rival spermatozoa from different male fish occurs differently in internally and externally fertilizing fish. In internally fertilizing fish, sperm from multiple males compete within the female's reproductive tract, following multiple inseminations during their breeding season and the female ovarian fluid exerts significant selection pressure on fertilization success (Lehnert et al., 2017; Parker, 2021). In externally fertilizing fishes, sperm competition occurs outside the female's reproductive tract, eggs are fertilized externally with minimal female control over sperm access. Overall, in both fertilizing systems, males with more competitive sperm achieve greater fertilization success (Gage et al., 2004; Malo et al., 2006; Kholodnyy et al., 2019). While early theoretical models predicted that increasing sperm production in sneaker male fish is an adaptive response to elevated sperm competition, empirical evidence supported this hypothesis and provided a comparative insight for examining the relationship between testis morphology, sperm production, and sperm quality across different fish taxa (Simmons & Fitzpatrick, 2012; Fitzpatrick & Lüpold, 2014; Parker et al., 2010). The positive correlation between sperm competition intensity and fish reproductive traits (sperm reserves, sperm count, proportion of motile and morphologically viable sperm) suggested that high sperm production under

intense competition may drive the evolution of smaller sperm and reinforce anisogamy in fish, particularly among sneaker males (Parker et al., 2010; Gomendio & Roldan, 2008; Tourmente et al., 2009).

Natural selection and genetic drift shape sperm competition, which significantly influences fish reproductive success and subsequently impacts population dynamics (Nielsen, 2005). Also, environmental, genetic, and phylogenetic factors shape sperm traits across fish taxa (Gomendio & Roldan, 2008; Tourmente et al., 2009). Behavioural adaptations to sperm competition play a critical role in sperm survival, fertilization and, reproductive success, genetic diversity, and species resilience to ecological changes (Gage et al., 2004; Anderson et al., 2005; Yeates et al., 2007). This review bridges the gap between micro-scale gametic physiology and macro-scale population dynamics and addresses how ecohydrological variability and biological stressors modulate sperm competition in fish together with fertilization success. By synthesizing previously existing environmental data on sperm motility sensitivity and fertilization kinetics, this study provides a mechanistic understanding of how recruitment fluctuations are often overlooked in traditional stock assessment models. Ultimately, this study offers essential insights for fisheries science and environmental management, providing a framework to establish evidence-based conservation strategies and hydrological standards necessary to preserve the reproductive viability and evolutionary resilience of aquatic populations facing anthropogenic and climatic pressures.

2.0 METHODOLOGY

2.1 Literature search and selection

The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework, which provides a robust and transparent structure for identifying, screening, and evaluating academic resources was adopted in this study. PRISMA criteria guided the inclusion of various publication types, including original research articles, systematic reviews, short communications, opinion pieces, and methodological evaluations. The steps in the selection of relevant literature are presented in (Figure 1). A comprehensive literature search was conducted across multiple databases, viz: Google Scholar (for gray literature), African Journals Online (AJOL), Web of Science, Data Citation Index, MEDLINE®, Science4Life, ScienceDirect, SpringerLink, JSTOR, and Scopus. Boolean operators were used to construct the search queries with combinations of the following keywords: sperm motility, sperm velocity; fish, teleost as a model; sperm competition, reproductive strategy, fertilization success; and biochemical, physiological, ecohydrology and physical factors influencing spermatozoa and fertilization success in fish

2.2 Inclusion/exclusion criteria, data extraction and synthesis

The search focused on peer-reviewed publications from 2000 to 2024 that examined relevant studies on sperm competition and reproductive biology in Teleostei and Chondrichthyes. Eligible studies included experimental, observational, and comparative research addressing sperm competition, sperm motility, fertilization, and fish reproductive traits. Studies involving mammals, amphibians, reptiles, and birds were excluded; non-English publications and articles lacking substantive data on sperm motility or sperm competition in fish were not included. Finally, a total of 177 articles were used for this review. Key data extracted from each study included species examined, sperm traits, mating systems, experimental conditions, and major findings. Thematic synthesis was then conducted by grouping results into two main categories: biological and ecohydrological factors influencing sperm traits.

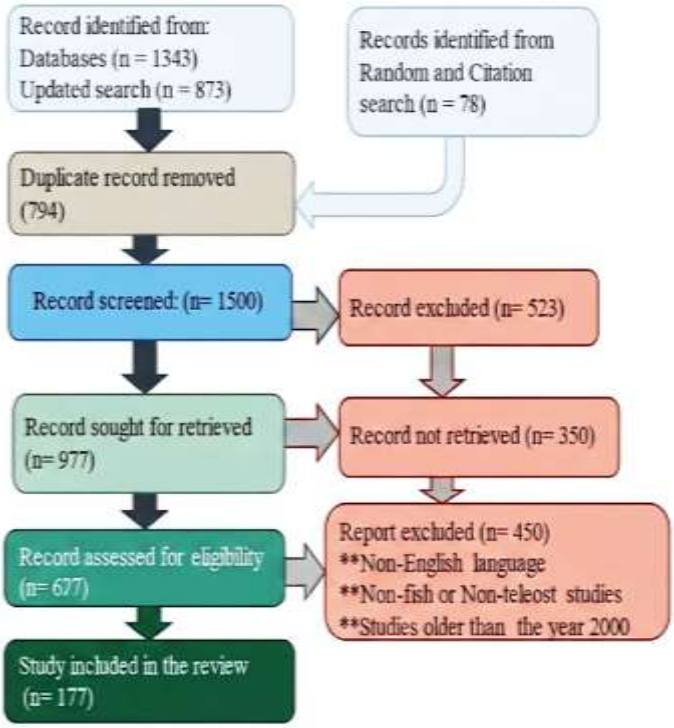

Figure **1.** Schematic representation for screening, inclusion and exclusion criteria.

3.0 RESULTS AND DISCUSSION

3.1 Biological factors affecting sperm traits and competition

3.1.1 Fertilization mode

Sperm competition and fertilization mode (internal vs. external) are key evolutionary drivers shaping sperm diversity in fish. However, among phylogenetically distant species, the correlation between fertilization mode and sperm traits does not consistently predict patterns of sperm competition or fertilization success (Immler et al., 2007; Zeng et al., 2014; Lüpold & Pitnick, 2018; Pitnick et al., 2009; Simpson et al., 2014). Despite this variability, fertilization mode significantly influences sperm length evolution across different fish taxa, including phylogenetically distant species (Kahrl et al., 2021; Isangedighi et al., 2024). Elongated head sperm morphology in internally fertilizing fish is a biological evolutionary adaptation for enhancing reproductive success, while short-headed sperm is an adaptation for fertilization success in externally fertilizing fish (Lehnert et al., 2017). The elongated morphology of sperm in internally fertilizing fish enhances hydrodynamic efficiency, facilitating progressive motility and successful navigation through the high-viscosity media of the female reproductive tract. In externally fertilizing species, a compact or spherical sperm head minimizes drag in low-viscosity aquatic environments, favouring rapid velocity and high-volume gamete production to maximize success in raffle-style sperm competition (Lüpold & Pitnick, 2018). These divergent sperm morphologies reflect a fundamental evolutionary trade-off, where selective pressures for penetrative capacity in high-viscosity internal environments are balanced against the mechanical requirements for rapid dispersal and high-volume output in external fertilization (Lüpold & Pitnick, 2018, Jacob et al., 2024b). The biological requirements of the fertilisation environment profoundly shape the sperm morphology of fish, as evidenced by comparative studies. The frequent occurrence of slender-headed forms in some externally fertilizing taxa suggests that sperm architecture is not only determined by fertilization mode, even if externally fertilizing species frequently display compact head morphologies to reduce hydrodynamic drag in aquatic media (Koya et al., 2011). This morphological plasticity implies that the main biological factor influencing sperm morphology and motility is post-copulatory sexual selection, particularly the level of sperm competition (Biagi et al., 2016; Ito et al., 2021; 2022). Therefore, more mechanistic investigation is required to clarify how environmental limitations and selection pressures interact to influence the evolutionary pathways of fish spermatozoa.

In Lake Tanganyika, cichlid species exhibiting internal fertilization demonstrate a positive correlation between sperm competition intensity and both total sperm length and swimming velocity. (Balshine et al., 2001; Fitzpatrick et al., 2009). This was confirmed by Fitzpatrick (2014), a meta-analysis, which revealed a multiple paternity rate in internally fertilizing fish compared to externally fertilizing individuals, reflecting elevated sperm competition in internally fertilizing fish. In this regard, proper estimation of sperm competition levels is important when comparing sperm traits across different fertilization modes and phylogeny, particularly among species within the same genus or family. This will provide clear insight into the evolutionary lineage influential effect on sperm competition in fish. Consequently, due to the relatively small number of internally fertilizing fish and limited data availability, this presents a challenge to identifying closely related internal fertilizers for direct comparison and prevents large-scale phylogenetic assessments of fertilization mode and its relationship to sperm competition in internal fertilizing fish. Integrating fish behavioral ecology into such comparisons is essential to infer the specific selective pressures that drive sperm trait evolution, thereby strengthening and complementing large-scale phylogenetic analyses.

3.1.2 Fish genital structure

The genital structure analyses in internally fertilizing and internal gametic association (IGA) fish, such as *Sebastes marmoratus* and *Apogon japonicus* revealed retracted, elongated, and slender genitalia within the abdominal cavity (Ramm et al., 2014; Kowalski & Cejko, 2019). In species such as *Ditrema temmincki* and *Sebastes cheni* that utilize internal fertilization, conspicuous copulatory organs are absent, though a small genital papilla is present (Immler et al., 2007; Parker, 2014). Despite morphological differences across species, phylogenetic generalized least squares (PGLS) analysis indicated that neither fertilization mode nor sperm competition level significantly affected fertilization success or relative genital length in these taxa (Ito et al., 2022). Even when controlling for phylogeny particularly in comparisons among closely related taxa, the correlation remains robust, suggesting that the evolution of genital structures is a primary driver of sperm morphological diversification, ultimately shaping fertilization efficiency and reproductive success in these fishes. (Koya et al., 2011; Ito et al., 2022; Muto & Kubota, 2009; Støstad et al., 2018). Other theoretical models combining hydrodynamic insight suggest that sperm with a head length-to-width ratio of approximately 2:1 experience lower drag than spherical heads (1:1), although extremely slender heads (e.g., >4:1) may incur increased drag (Humphries et al., 2008). While externally fertilizing fish encounter selective pressures related to ovarian fluid viscosity. Upon spawning, their eggs are often surrounded by a coating of ovarian fluid, which can vary in thickness and composition across species. In *Hemitripterus dybowskii*, elongated-headed sperm are thought to be an adaptive response to a viscous medium, enhancing motility and fertilization efficiency (Zadmajid et al., 2019; Ito et al., 2022). By contrast, *Acanthopagrus flavidus*, another externally fertilizing species, produces sperm with more oval-shaped heads, demonstrating that sperm morphology in externally fertilizing fish is not uniform but instead reflects species-specific adaptations to ecological and reproductive constraints (Mirnamniha et al., 2019). This intra- and interspecific variation in sperm morphology reflects the complex selective pressures acting on sperm traits in both internal and external fertilizing fish. Despite the growing interest in sperm competition, most studies have narrowly focused on these two fertilization modes, while overlooking other reproductive strategies such as hermaphroditism, parthenogenesis, and hybridogenesis (Vladic & Järvi, 2001; Pitnick, et al., 2009). The prevalence of sexual reproduction in fish is driven by the evolutionary necessity of meiotic recombination to purge deleterious mutations and maintain genetic diversity for environmental adaptation. Consequently, the reliance on sexual strategies over asexual alternatives complicates fisheries management, as skewed population structures or disrupted mating systems can severely impact reproductive potential and stock resilience (Lehnert et al., 2017). Incorporating these underrepresented fertilization modes into future research will provide a more integrative framework for understanding the evolutionary dynamics of sperm competition, fertilization strategy, and reproductive morphology across different fish taxa (Lehnert et al., 2017; Mirnamniha et al., 2019).

3.2 Ecohydrological variables

3.2.1 Effect of temperature on fish spermatozoa

Environmental temperature regulates sperm physiology, competition and fertilization in fish (Williot et al., 2000). Sperm motility is an energy-dependent process, primarily fueled by intracellular adenosine triphosphate (ATP). Hence, elevated environmental temperature accelerates ATP depletion, leading to increased velocity and shorter motility duration. In contrast, lower temperatures tend to reduce sperm velocity but extend the overall motility period, reflecting a trade-off between speed and longevity (Gage et al., 2004; Echi et al., 2009; Alavi et al., 2011; Isangedighi et al., 2025). In a comparative study, Alavi and Cosson (2006) demonstrated species-specific thermal responses in *Ctenopharyngodon idella* and *Cyprinus carpio*. Their study revealed that Grass carp spermatozoa maintain motility longer at 20 °C than at 26 °C in common carp, highlighting interspecific differences in thermal sensitivity. These temperature-driven variations in sperm traits are crucial determinants of reproductive success under sperm competition, particularly in externally fertilizing species, where fertilization occurs in open water. Minor deviations from the species-specific optimum temperature may drastically affect sperm velocity, motility duration, and overall fertilizing capacity (Alavi et al., 2011; Jacob et al., 2024b; Obot et al., 2025).

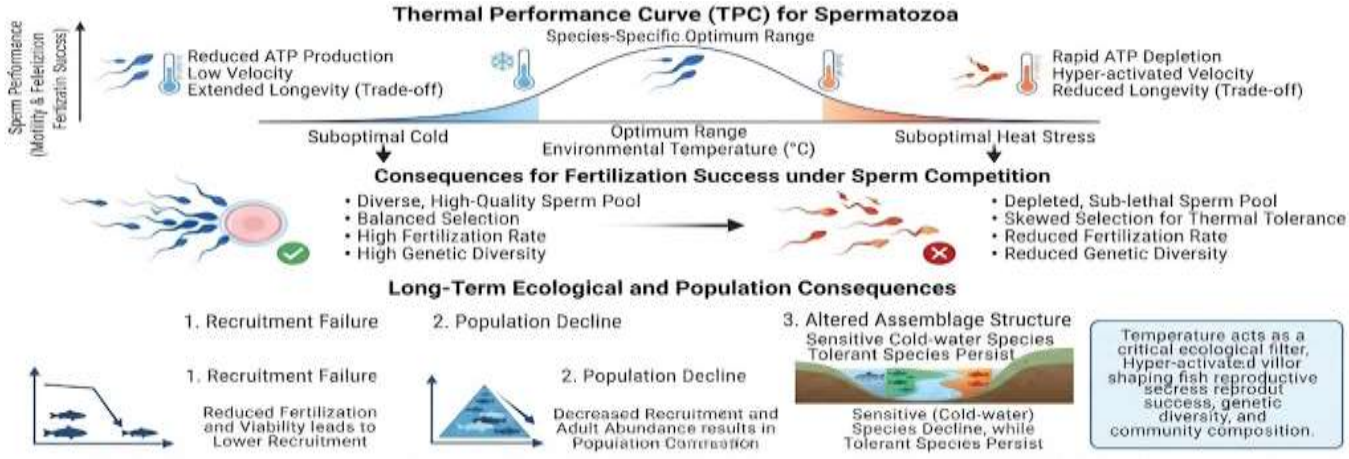

Figure **2**. Conceptual model of the multi-level consequences of thermal stress on fish spermatozoa, reproduction and population.

Vladic & Järvi (2001), Observed that higher temperatures reduced sperm longevity in *Salmo trutta*, disadvantaging late-arriving or stored sperm in competitive fertilization events (Figure 2). Furthermore, studies employing computer-assisted sperm analysis (CASA) confirm a unimodal (bell-shaped) relationship between temperature and sperm performance across multiple fish species, with both suboptimal low and high temperatures impairing motility, viability, and competitive ability (Kime et al., 2001). These thermally mediated effects on sperm performance are of increasing ecological concern under current environmental pressures, particularly in tropical aquatic ecosystems. Anthropogenic impact, climate change, and

habitat fragmentation are altering aquatic thermal regimes at unprecedented rates. Such changes may impose selective pressures that shift sperm trait evolution, alter patterns of sexual selection and reproductive success at the population level for both temperate and tropical fishes (Fenkes et al., 2017; Jacob et al., 2023; Isangedighi et al 2024; Jacob et al., 2024a). Collectively, these findings revealed that temperature is not merely a physiological factor, but as an ecological force shaping sperm competition outcomes in natural fish populations, especially in thermally dynamic or anthropogenically disturbed habitats. Rising aquatic temperatures driven by climate change represent a critical threat to reproductive dynamics in fish, particularly through their impact on sperm competition (Jacob et al., 2023; Isangedighi et al 2024; Jacob et al., 2024b). Many species, including *Salmo trutta*, *Neogobius melanostomus*, and *Oreochromis niloticus*, narrow thermal optima are required for sperm function. As such, even short-term exposure to elevated temperatures during spawning can significantly enhance fertilization success. Thermal stress reduces sperm motility, velocity, and longevity, which are key determinants of competitive fertilization that potentially reshape sexual selection by favouring males whose gametes possess greater thermal resilience (Fenkes et al., 2017).

However, responses to temperature stress are highly species-specific. Cold-water species, such as salmonids, which depend on extended sperm motility durations, are particularly vulnerable to warming temperatures. In contrast, tropical fishes like cichlids exhibit broader thermal tolerances but may still experience sub-lethal reductions in sperm quality under elevated temperatures (Rurangwa et al., 2004; Jacob et al., 2024a).

These interspecific differences may suggest that climate-driven thermal shifts could disproportionately influence sperm competition outcomes across fish assemblages, resulting in skewed reproductive success, diminished genetic diversity, and altered population dynamics (Fenkes et al., 2017; Isangedighi et al., 2024; Obot et al., 2025). Moreover, thermal stress rarely acts in isolation. When compounded by additional environmental pressures such as pollution from anthropogenic sources-agrochemicals, industrial effluent, eutrophication, or hypoxia the adverse effects on sperm performance and reproductive capacity may be significantly amplified. Such synergistic stressors may accelerate reproductive declines, particularly in thermally sensitive or ecologically constrained species (Obot & Jacob 2024, Jacob et al., 2024b). These insights are integral for predicting the evolutionary and ecological consequences of global climate change on aquatic fauna.

3.2.2 Influence of pH on sperm motility

The initiation and maintenance of sperm motility in fish are regulated by a combination of extracellular and intracellular pH of the surrounding medium (Tiersch & Yang, 2012). Extracellular pH, particularly, plays a critical role by modulating intracellular proton concentrations, which influence membrane potential and affect flagella activity and motility (Filiz, 2018; Sanchez et al., 2024). Numerous studies have identified pH as a key ecohydrological parameter impacting sperm quality, maturation, motility, and fertilization success (Lahnsteiner & Mansour, 2012; Marion et al., 2014; Wojtczak et al., 2007; Ciereszko et al., 2010). As spermatozoa transit the sperm duct, the microenvironment of the seminal plasma characterized by regulated pH and specific ionic concentrations, maintains cells in a state of quiescence, thereby preserving their motility potential until the moment of spawning. Experimental studies involving spermatozoa incubation in artificial seminal plasma revealed that fluctuations in pH can profoundly affect sperm motility (Ingermann et al., 2002; Woolsey et al., 2006). The optimal pH range for sperm activation and motility differs among fish species Table 1. Also, external media or ovarian fluid with alkaline pH levels promote motility initiation and enhance fertilization success (Wojtczak et al., 2007; Lahnsteiner, 2002).

Table **1.** Optimal pH range for different fish spermatozoa and their role in motility

Fish Species	Optimal pH Range	Role in Sperm motility
Atlantic Salmon (*Salmo salar*)	8.0–9.0	Sperm motility initiation is strictly pH-dependent and alkaline conditions trigger high-velocity activation.
Common Carp (*Cyprinus carpio*)	7.5–8.5	High motility observed in buffered alkaline media; acidic conditions inhibit the activation process.
Rainbow Trout (*Oncorhynchus mykiss*)	8.0–9.5	Sperm show peak motility in alkaline environments; internal pH increases rapidly upon activation.
Milkfish (*Chanos chanos*)	7.8–8.2	Optimal motility achieved in slightly alkaline, saline media that mimic seawater conditions.
Yellowfin Tuna (*Thunnus albacares*)	7.5–8.0	Sperm are highly sensitive to pH; alkaline buffers are essential for maintaining motility during in vitro handling.
Lates calcarifer	7.4–7.8	Alkaline storage media enhance motility post-chill storage.
Epinephelus malabaricus	7.8–8.0	Highest motility at near-neutral/alkaline pH; declines outside this range.
Salmo trutta	~10	High pH enhances velocity and duration; declines sharply at lower pH.
Acipenser persicus	~8.0	Alkaline solutions support both motility initiation and maintenance.
Anguilla anguilla	7.8–8.1	Acidification reduces motility; neutral–alkaline media support activation.

However, the role of pH in sperm motility initiation is closely related to sperm membrane potential, in which acidic conditions can lead to depolarization of the sperm plasma membrane, thereby rendering spermatozoa immotile (Alavi et al., 2019). In contrast, an increase in external pH can stimulate intracellular cyclic AMP (cAMP) production, facilitating motility initiation. However, membrane hyperpolarization following activation does not always coincide with an increase in intracellular pH (Filiz, 2018; Isangedighi et al., 2024). In externally fertilizing species, the pH of the ambient water is a critical determinant of sperm motility. This effect is species-specific and varies with the pH range. For instance, in Serranidae, alkaline pH conditions are generally favoured for sperm motility and significant deviations from this optimal pH range can impair motility (Frommel et al., 2010; Haq et al., 2011; Sanchez et al., 2024). Alaenazi et al. (2024), reported that in *Epinephelus malabaricus*, reduced sperm motility duration occurred following low pH conditions, but improved at pH 7.8–8.0, demonstrating an optimal pH window for sperm performance in this species.

On the other hand, extreme pH conditions can disrupt sperm plasma membrane composition, thereby compromising both viability and motility because sperm function during fertilization is highly dependent on enzymatic activity and particularly sensitive to pH alteration (acidic or alkaline) (Filiz, 2018; Park et al., 2022). Altered environmental pH can disrupt the structural integrity and functionality of the sperm flagellum, leading to reduced propulsive force generation, which limits sperm motility and egg penetrating capacity during fertilization (Kowalski & Cejko, 2019; Park et al., 2022). Similarly, exposure to highly acidic conditions (e.g., pH 2–4) can lead to irreversible cellular damage, resulting in complete motility loss and apoptosis. In marine species such as *Gadus morhua*, ocean acidification has been linked to diminished sperm motility and reduced fertilization potential, highlighting the broader ecological consequences of declining ocean pH levels (Frommel et al., 2010).

In freshwater fish, sperm activation is typically facilitated by media with an alkaline pH. Alkaline environments have been shown to support optimal sperm motility in many freshwater species (Krasznai et al., 2003). However, in rainbow trout *Oncorhynchus mykiss*, the specific role of alkalinity in sperm activation and sustained motility is not fully understood, prompting further investigation into species-specific responses, particularly in the context of short-term in vitro sperm storage. Finally, a comprehensive understanding of both internal and external pH requirements for sperm activation, motility, and fertilization across different fish species is essential in aquaculture for cryopreserved sperm utilization, optimizing activation media, and thereby ensuring reproductive success in both cultured and wild fish populations.

3.3 Effects of ions in sperm competition

3.3.1 Effects of potassium ions in sperm activation and motility in fish

The role of the different ions in regulating sperm motility is presented in Table 1. However, among the specific ions, potassium ion concentration ($[K^+]$) plays a significant role in regulating sperm activation and motility across fish taxa. For example, in salmonids, sturgeons and paddlefish, $[K^+]$ serves as a key physiological switch for initiating or suppressing sperm motility (Krasznai et al., 2003). The extracellular potassium ion concentration ($[K^+]_o$) within the seminal plasma of salmonids is responsible for maintaining spermatozoa in a quiescent state. Motility is triggered when sperm are released into a K^+-free medium, highlighting the inhibitory role of $[K^+]_o$ in vivo (Wang et al., 2021). This motility activation is associated with a rapid increase in cyclic adenosine monophosphate (cAMP) levels shortly after exposure to K^+-free conditions, suggesting a signalling cascade involving membrane depolarization and second messenger activation (Krasznai et al., 2000). Although the precise mechanistic relationship between $[K^+]_o$ and cAMP has not been completely explained in both theoretical and empirical analyses, sperm motility activation is tightly linked to K^+ efflux.

Potassium channel blockers such as tetraethylammonium (TEA^+), nonyltriethylammonium, Ba^{2+}, and Cs^+ inhibit motility initiation in salmon spermatozoa through suppression of K^+ conductance across the sperm membrane. Therefore, hyperpolarization of the sperm membrane via transmembrane K^+ efflux is a fundamental trigger for activating axonemal movement in salmonids (Kho et al., 2001). Furthermore, Linhart et al. (2003), demonstrated that K^+ exerts direct effects on demembranated flagella and axonemal structures, suggesting an additional, possibly structural role in modulating motility. In sturgeons and paddlefish, although detailed molecular mechanisms are not completely characterized, similar observations among individual salmonids have been reported. Alavi et al. (2011), reported an average potassium concentration of 6.92 ± 0.88 mmol/L in the seminal plasma of *Acipenser persicus*, which elevated K^+ levels, inhibiting sperm motility. Moreover, high concentrations of K^+ in cryopreservation media can significantly impair post-thaw motility in cyprinids and sturgeons, further highlighting the critical role of ionic balance in sperm function.

3.3.2 Role of calcium ions (Ca^{2+}) and magnesium ions (Mg^{2+}) on sperm motility

Calcium ions (Ca^{2+}) play a crucial role in regulating sperm motility by triggering the activation of flagellar movement. The binding of Ca^{2+} to the axonemal structures of the flagella induces bending and contraction, generating the characteristic whip-like motion that propels sperm forward. In cyprinid species, extracellular calcium ($[Ca^{2+}]_o$) is essential for initiating sperm motility (Cox & Logan, 2021). Krasznai et al. (2000) reported enhanced motility in carp sperm 30 seconds after exposure to a solution containing 10^{-4} M NaCl. Similarly, demembranated sperm treated with Triton X-100 exhibited high motility in the presence of 10^{-6} to 10^{-5} M Ca^{2+} (Kowalski & Cejko, 2019). Inhibitory studies using verapamil, a calcium channel blocker, further confirmed the role of Ca^{2+} in motility initiation (Dzyuba et al., 2019). In mature carp sperm, pre-diluted and incubated in a physiological solution (140 mM NaCl, 10 mM KCl, 1 mM $CaCl_2$, 20 mM HEPES, pH 8.5), verapamil suppressed motility by preventing the rise in intracellular calcium concentration ($[Ca^{2+}]_i$) (Ghaniei et al., 2018). This suggests that Ca^{2+} influx through specific membrane channels is essential for activating motility (Table 2).

Table **2.** Role of some specific ions in sperm functions and motility

Ions	Roles in sperm motility, competition and fertilization	Reference
Potassium ions (K^+)	Enhance acrosomal reaction, support sperm quality, and motility	(Fallah et al., 2018).
Calcium ions (Ca^{2+})	Enhance acrosomal reaction, increase sperm quality, capacitation, motility, ensure spermatogenesis, and support sperm morphology.	(Eyo, et al., 2009; Mirnamniha et al., 2019; Beigi Harchegani, 2019)
Magnesium ions (Mg^{2+})	Improve Sperm quality, capacitation, and motility; increase spermatogenesis and sperm morphology.	(Azab *et al.,* 2021)
Sodium ions (Na^+)	Increase acrosomal reaction, sperm quality, capacitation, and motility.	(Jiménez et al., 2011; Beg et al., 2020)
Chloride ion (Cl^-)	Improve sperm motility, capacitation, acrosomal reaction, and sperm volume.	(Liu et al., 2017)

On the other hand, Extracellular Ca^{2+} may enter through sperm-specific calcium channels (CatSper), triggering the release of intracellular Ca^{2+} from internal stores via calmodulin-mediated signalling (Azab et al., 2021). Channel blockers such as flunarizine and conotoxin have been shown to reduce $[Ca^{2+}]_i$ and suppress sperm activation in common carp (Krasznai et al., 2000). However, in *Oreochromis mossambicus*, intracellular Ca^{2+} is vital not only for sperm motility initiation but also for motility maintenance (Morita et al., 2004). Studies using Ca^{2+}-sensitive fluorescent probes further demonstrated that increased $[Ca^{2+}]_i$ prolongs the duration of sperm motility (Krasznai et al., 2000). Although the relative contributions of extracellular Ca^{2+} influx and intracellular Ca^{2+} release to sperm activation require further investigation across species and specific habitats, environmental calcium levels can initiate sperm motility under natural conditions. For example, Freshwater spawning environments facilitate essential Ca^{2+} influx across the sperm plasma membrane, providing the precise ionic conditions required for physiological activation (Alavi et al., 2011; Cabrita et al., 2014; Beigi Harchegani et al., 2019).

The role of magnesium ions (Mg^{2+}) in teleost sperm motility remains underexplored compared to other ions such as Ca^{2+}. However, available evidence suggests that Mg^{2+} contributes significantly to sperm activation and motility, particularly in demembranated spermatozoa. Khara (2014) reported enhanced sperm motility in *Ctenopharyngodon idella* (grass carp) following exposure to various concentrations of $MgCl_2$. Similarly, Lim et al. (2012) found improved motility parameters in *Larimichthys polyactis* spermatozoa at 0.2 M $MgCl_2$, indicating that Mg^{2+} plays a role in activating motility. However, concentrations of $MgCl_2$ exceeding 0.2 M were associated with a significant decline in motility duration, suggesting a dose-dependent inhibitory effect (Khara, 2014). In internal fertilization perspective, variations in Mg^{2+} and Ca^{2+} concentrations within the seminal plasma may compromise semen quality and fertility (Ghaniei et al., 2018). This observation highlights the need for future studies investigating the synergistic effects of these ions on sperm competition and fertilization success across both externally and internally fertilizing fish.

3.4 Role of osmolality in the initiation of sperm motility

Osmotic pressure of the internal and external environment controls the activation of sperm motility in teleost fishes. Exposure to either hypo-osmotic or hyperosmotic environments can trigger sperm motility initiation, depending on the species ecological and reproductive adaptations. For example, in freshwater fish family Cyprinidae (goldfish, common carp, and crucian carp), their spermatozoa become motile when released into hypotonic environments. Alavi et al. (2006), reported that goldfish, common carp, and crucian carp sperm remain quiescent when diluted in iso-osmotic solutions of NaCl, KCl, mannitol, or glucose, each with osmolarity comparable to seminal plasma (~300 mOsm kg^{-1}). However, motility was rapidly initiated when their sperm were introduced into media with osmolality below 200 mOsm kg^{-1}, indicating that hypotonic shock serves as a physiological trigger for motility activation. This implies that in vivo, sperm motility is suppressed within the sperm duct due to the relatively high osmolality of the seminal plasma, which prevents premature activation across freshwater fish species (Khara, 2014).

In contrast, marine species exhibit an opposing osmotic response, whereby hyperosmotic conditions of the plasma membrane, together with an osmolarity of about 300 mOsm kg^{-1}, keep fish spermatozoa in a quiescent stage. Sperm become motile when exposed to seawater with osmolality reaching 1200 mOsm kg^{-1} (Yang et al., 2009). The hyperosmotic environment induces intracellular changes, including elevated potassium (K^+) and calcium (Ca^{2+}) levels, as well as internal acidification within the sperm cytoplasm. These modulations act as molecular signals for motility initiation under marine conditions. In internally fertilizing freshwater fish such as the ocean pout (*Macrozoarces*

americanus), sperm motility is initiated under isotonic conditions, reflecting the osmolality of the female reproductive tract. Notably, neither hypotonic nor hypertonic environments are effective in initiating motility in *Macrozoarces americanus*, underscoring a specialized adaptation to internal fertilization (Huang et al., 2004; Yang et al., 2009). In marine fish, once spermatozoa are released in the seawater and activated, sperm exhibit prolonged motility and remain active for up to one week, compared to externally fertilizing freshwater species (Hu, 2005).

Moreover, in euryhaline species such as medaka (*Oryzias latipes*), they exhibited a broad osmotic tolerance for sperm motility activation. Motility can be initiated across a wide range of osmolalities, including deionized water (~25 mOsm/kg) and Hanks' balanced salt solution (HBSS) with osmolalities ranging from hypotonic (92 mOsm/kg) to hypertonic (686 mOsm/kg) (Yang et al., 2009). This flexibility reflects the species' ability to reproduce across diverse saline environments. Tilapia (*Oreochromis niloticus*) also shows a similar but more restricted osmolarity pattern. In freshwater-acclimated *Oreochromis niloticus*, sperm motility is triggered in media with osmolarity ranging from 0 to 400 mOsm/kg, regardless of the electrolytes presence. In seawater-acclimated tilapia, sperm motility initiation occurs within a broader osmolality range of 0–500 mOsm/kg, particularly in NaCl solutions supplemented with 10 mM HEPES buffer (Morita et al., 2004).

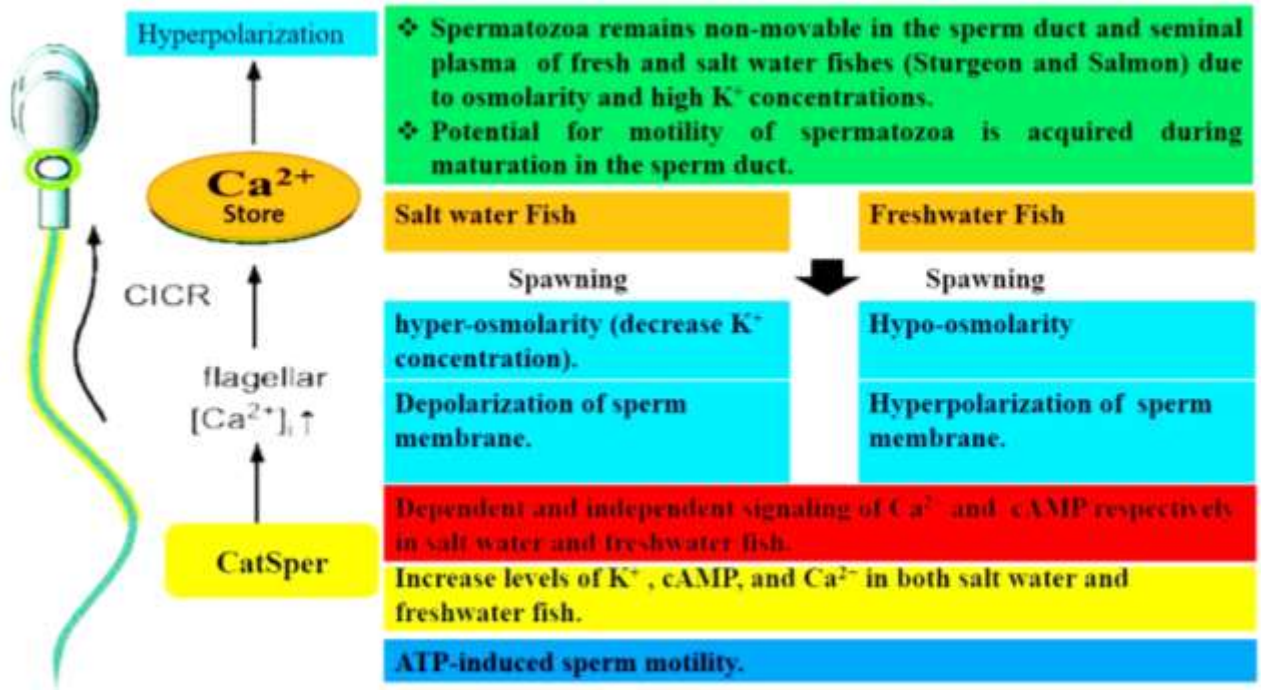

Figure **3**: Mechanisms of environmental factors-induced activation and motility kinetics in fish spermatozoa.

Interspecies variation in motility duration is largely attributed to differences in intracellular ATP reserves and creatine phosphate concentrations, which fuel flagella activity (Alavi et al., 2021). In marine species, hyperosmotic conditions and elevated ionic concentrations in seawater trigger the activation of sperm flagella upon ejaculation. The sudden shift in osmolarity causes rapid water and solute fluxes across the sperm membrane, which are regulated by aquaporin water channels enhances maintenance of cellular homeostasis. Concurrently, the influx of Ca^{2+} initiates intracellular calcium signaling cascades essential for motility activation. Membrane deformation from osmotic stress also activates stretch-activated channels (SACs), which contribute to ion exchange and water efflux (Krasznai et al., 2003). The resulting activation of dynein ATPase under optimal intracellular ionic conditions triggers axonemal bending and flagellar motion. However, the rapid depletion of intracellular ATP, coupled with a progressive increase in internal ionic concentration, may reduce dynein motor efficiency and consequently limit/reduce sperm swimming and motility duration.

3.5 Physiology of sperm motility

Sperm quality is primarily assessed by evaluating motility and fertilization success (Sheng et al., 2014). In the seminal duct and under resting conditions, spermatozoa remain immotile. Motility is triggered only after sperm are released into the aquatic environment, where activation is induced by various external factors (Alavi et al., 2021). Numerous studies on finfish and shellfish have documented the physiological mechanisms underlying sperm activation in both marine and freshwater species (Zhu et al., 2006; Wang et al., 2012) (Figure 3). Among the most influential environmental factors regulating sperm activation and motility are water temperature, pH, salinity, osmolality, viscosity, and the ionic composition of the surrounding medium (Alavi & Cosson, 2006; Alavi et al., 2009). The duration of sperm motility in fish is generally brief following activation in the aquatic environment, typically ranging from a few seconds to several hours, depending on the species, except in some marine species (Dzyuba et al., 2019; Kowalski & Cejko, 2019; Alavi et al., 2021).

Conclusion

Both theoretical frameworks and empirical studies have highlighted the complex and often non-linear relationships between sperm competition and reproductive success in fish, with no consistent directional trends across species. This highlighted the need for targeted, species-specific investigations to reveal the relative influence of individual biological and ecohydrological factors on fertilization dynamics during sperm competition. Environmental constraints such as fluctuations in temperature, pH, specific ions, and osmolarity can disrupt sperm function in fish with cascading effects at the population level. In species where reproductive output is tightly coupled to sperm motility and viability, such disruptions may lead to reduced fertilization success, biased paternity, decreased population sizes and diminished genetic diversity and compromised adaptive potential, increasing vulnerability to environmental change. These risks are particularly acute in fisheries-dependent communities and externally fertilizing species, where the intensity of sperm competition is high, with resultant declines in recruitment and stock productivity and jeopardizing long-term sustainability. Therefore, a mechanistic understanding of how ecohydrological variables mediate sperm competition is essential for improved predictions and management of reproductive resilience under changing climate conditions. Integrating species-specific sperm thermal thresholds into aquaculture protocols, spawning habitat management, and conservation breeding programs is crucial to ensure reproductive success. Moreover, incorporating sperm biology into ecological risk assessments can inform temperature- and stress-sensitive conservation strategies, particularly in tropical freshwater systems threatened by eutrophication, pollution, and habitat degradation.

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