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The Faculty of Fisheries and Protection of Waters

Laboratory of Reproductive Physiology

BACHELOR'S THESIS

ADVANCES IN FISH SPERM CRYOPRESERVATION: TAXONOMICAL CONSIDERATION

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Theses guidelines

Application of low-temperature sperm storage (cryopreservation) nowadays is considered as powerful tool in agriculture, medicine and conservation biology. This methodological approach is aimed to preserve gene pool of unique populations protecting them from loss of genetic variability and extinction. To get viable sperm samples after low temperature storage, species specific protocols should be developed.

Fishes are the most numerous species vertebrate group, taxonomically containing representatives of different classes, but their abundance and diversity are in decline due to human activity. At the same time, they are source of 14-17 % of animal protein consumption by human population. That is why the application of sperm cryopreservation would benefit for aquaculture and fish conservation measures. Sperm cryobanking in fish is also important because cryopreservation of eggs and embryos nowadays is impossible due to their specific biological properties but restoration of individuals is possible by androgenesis in fish. Big diversity of fish reproductive systems makes application of cryobanking methodology in fish conservation quite complicated because species-specific protocols of long-term storage are required. Until 1990 success in fish sperm cryopreservation was reported for approximately 200 fish species. From that time, no update is available. Moreover, the rate of application of sperm cryopreservation in aquaculture is much lower than in cattle breeding.

This bachelor study is aimed to explore the current state of fish sperm cryopreservation in relation to aquaculture and conservation measures. The work will be performed by intensive study of available via Internet information, taking into account basic knowledge on cryobiology and fish taxonomy.

Scope of work report:	**30 – 50 pages**
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Recommended resources:

Cabrita, E., Sarasquete, C., Martínez-Páramo, S., Robles, V., Beirão, J., Pérez-Cerezales, S., Herráez, M.P., 2010. Cryopreservation of fish sperm: applications and perspectives. Journal of Applied Ichthyology 26, 623-635.

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Content

1. Introduction

The first successful cryopreservation of fish sperm was made 66 years ago by Blaxter (Blaxter, 1953). Despite the fact that the possibility of long-term storage of gametes represents great opportunities in improving aquaculture techniques, cryopreservation of fish sperm has some complications that violate to achieve such level of results as does the cryopreservation in cattle breeding. According to Terrence R. Tiersch (2008), during the same time after first reported successful cryopreservation of livestock sperm it became a popular tool and turned into a billion-dollar global industry, while cryopreservation of aquatic species sperm remains a research activity with little commercial application.

The main difficulty consists in problems resulting from fish diversity. It is necessary to clarify that due to the fact that different taxonomic groups fit the definition "fish" in present work this group will be limited to the subclass Actinopterygii. Gamete morphology and biology within this diverse and abundant group vary among species; therefore the cryopreservation strategies also vary accordingly (Labbé et al., 2013). Single universal cryopreservation protocol cannot be offered so far (Rana, 1995).

Hundreds of references to sperm cryopreservation in aquatic species are available today but the high diversity of published cryopreservation methods complicates their evaluation (Labbé et al., 2013). To simplify the issue some minor variables should be excluded from methods intended for hatchery purposes. At the same time some factors cannot be ignored, because even insignificant difference in cryopreservation process characteristics can also affect results. The lack of standardization in practices and reporting is the most important barrier to expanded application of cryopreservation (Tiersch, 2008).

To date, the exact number of fish species for which sperm cryoprotocols are developed is unclear and there is no published full list of them. Nevertheless the number of existing protocols is sufficient to undertake some analysis.

The goal of this work is to review the current state of fish sperm cryopreservation in relation to conservation measures and aquaculture practice with special focus on taxonomical position of involved species.

2. Main part

2.1. Long-term storage of fish sperm

Cryopreservation is a long-term storage of living biological objects with the possibility of restoring their biological functions after thawing (Fuller et al., 2004). The typical storage temperature is -196 °C (the temperature of liquid nitrogen, that is a convenient for low temperature storage, not expensive, medium (Jamieson, 1991). At these values of temperature almost all molecules become motionless and, therefore, all biochemical reactions are stopped including those that lead to aging (Mazur, 2017). Despite the concerns that some events at atomic level can still take place in these conditions, or genetic information may be damaged by existing background radiation, it is of general consent that ultralow temperature storage, including freezing of samples and their thawing, is the only possible procedure to conserve cells' functional properties for long term (Cugia et al., 2011; Garman, 2003), virtually indefinitely (Jamieson, 1991).

2.1.1. History of fish sperm cryopreservation

The first successful cryopreservation of fish sperm was made by Blaxter in 1953 (Blaxter, 1953). It was preceded by discovery of cryoprotective properties of glycerol in 1949 (Polge et al., 1949), which is considered as a defining step in development of cryobiology as a science. It was a time of empirical, but important discoveries. Further, fusion of physics and biology has led to serious efforts to understand freezing injury in biological systems. Jim Lovelock was probably the first "real" cryobiologist with biophysical credentials, and the discovery of dimethyl sulfoxide (Me_2SO) by Lovelock and Bishop (1959) was based on rational prediction (Mazur, 2004).

Hundreds of scientific papers on fish sperm cryopreservation have been published around the world (Tiersch, 2008). A great effort was devoted to creating new and improving existing protocols. An interest in applied cryobiology is constantly growing. Useful applications are an important result of research without which basic studies become an academic luxury (Mazur, 2004). For cryobiology in particular, applications are everything, and it is no wonder that this has been the emphasis right from the

beginning (Mazur, 2004). Perhaps the most destructive side effect of this trend is the emergence of ‘intellectual property” as something to be held close to the chest, to remain secret, unpublished and unshared until patented, and even then to be leaked out slowly (Mazur, 2004).

2.1.2. Cryopreservation of fish sperm in aquaculture

The possibility to store fish sperm during long period of time can be an important tool in aquaculture. Barrie Jamieson and Terrence R. Tiersch in their fundamental works discussed important improvements which could be made in fish industries by application of sperm cryopreservation. They also underlined the significant potential of cryopreservation in the conservation projects for threatened and endangered species and other areas.

These improvements include: 1) saving the funds for maintenance of stocks by excluding the need to keep males; 2) continuous supply of gametes for optimal utilization of hatchery facilities or for experimental work; cryopreservation can be used to improve existing hatchery activities by providing sperm on demand and thus simplifying the time management of artificial spawning; 3) cryopreservation opens the prospects for genetic improvement via; creation of improved lines and control the genetic resources available for aquaculture; 4) cryopreservation eases the transportation of genetic materials between hatcheries; 5) it allows the restoration of genetic material (valuable genetic lines e.g. from endangered species, research models or improved farmed strains) in case of broodstock loss; 6) using of cryopreserved sperm of aquatic species may become an entirely new industry itself (Jamieson, 1991; Tiersch, 2008).

It is rather difficult to estimate the level of fish sperm cryopreservation application in practice of fisheries today. But it can be assumed, that in most common fish hatcheries it does not present an ordinary issue. The introduction of new technology is always associated with risk. For ordinary fish hatcheries it means an additional expenditure of energy, funds and time. The owner of the hatchery may need a cogent argument for introduction of this practice. One such reason could be the high cost of males per se or their keeping in captivity. If we are talking about a rare species, a rare breed, late maturing fish or the results of experimental work, introduction of method that would secure existing genetic material in vitro would be an acquitted risk. For

example, the high cost of keeping stud bulls was one of the decisive factors that made cryopreservation of livestock sperm in animal husbandry a billion-dollar global industry. Despite the numerous benefits that long term storage of gametes can bring to aquaculture, the sperm cryopreservation of aquatic species remains a research activity with little commercial application so far (Tiersch, 2008).

2.1.3. Genetic bank research programs and cryobanking of fish germplasm

Gene bank research programs can be organized with two quite different objectives in mind. The first one is the creation of collection of cryopreserved somatic tissues, cell lines and DNA samples from diverse species without intention to breed new individuals with this material. The second objective is explicitly aimed towards animal breeding. This type of genetic resource bank surely contains gametes and embryos; nevertheless, with the development of cloning technology a move away from the need to preserve only reproductive cells becomes possible (Watson and Holt, 2000).

Moreover, there is a notion, that the preservation of germ plasma should be a top priority among the many goals of cryopreservation (Chao and Liao, 2001).

Term "germplasm" broadly refers to the hereditary material transmitted to the offspring through germ cell. The concept that underlies the establishment and use of germplasm resource banks is essentially very simple. If gametes are maintained in a state of metabolic arrest, e.g. using cryopreservation, they could be used to support natural breeding programs (Watson and Holt, 2000).

Cryopreservation is considered as one component in an effective strategy to save endangered species by facilitating the storage of their gametes in a gene bank (Gausen, 1993; Chao and Liao, 2001).

<u>European cryobanks of aquatic species</u>

Several cryobanks were established in Europe over the last 30 years, with a common purpose of conservation of the genetic diversity from wildlife and farmed resources. Furthermore, almost every fish research institute has its own cryobank, often in the form of few liquid nitrogen tanks (Martínez-Páramo et al., 2017). Because of the lack of standardization an exhaustive list of those banks is difficult to establish. The

same problem can be observed in inability of general assessment of the quality of the collections.

Among the first in Europe, cryobanking of farmed fish sperm was launched in Czech Republic in 1996 as a part of the National program of conservation and use of farm animal genetic resources. The objective was to keep old less productive breeds as a part of national heritage and a source of genes for future breeding. The Cryobank was established in the Research Institute of Fish Culture and Hydrobiology (RIFCH), part of the nowadays Faculty of Fisheries and Protection of Waters in Vodnany. Altogether, sperm samples from 11 breeds of carp, seven breeds of tench, three breeds of wels catfish, three breeds of trouts and two species of sturgeons are stored (Martínez-Páramo et al., 2017). Besides genetic resources, fish sperm cryopreservation is also used for international scientific cooperation and commercial purposes (Martínez-Páramo et al., 2017).

2.2. Basic knowledge of cryobiology

Water is the most abundant molecule in a cell, accounting for 70 % or more of total cell mass. Consequently, the interactions between water and the other constituents of cells are of central importance in biological chemistry. A basic principle of cryobiology is that the extent of freezing damage depends on the amount of free water in the system and the ability of that water to crystallize during freezing (Fuller et al., 2004).

Typically, small isolated cells may tolerate freezing. Compacted fish spermatozoa with a reduced cytoplasmic compartment also tolerate cryopreservation (Labbé et al., 2013). Cryopreservation of marine fish semen normally presents better results for motility rate and fertilizing capacity after thawing than in freshwater species. This may be associated with greater resistance that show marine species to variations of osmolality than freshwater species (Magnotti et al., 2018).

Nevertheless, the process of cryopreservation is accompanied by arising of critical events in the cell, many of which may lead to its non-reversible damage or even death. The main critical steps of cryopreservation include cooling, freezing, and thawing (Labbé et al., 2013).

2.2.1. Cryoinjuries

When cells undergo freezing they are subjected to stresses resulting from the water-solute interactions that arise through ice formation (Mazur, 1984). Individual causes of cryoinjuries are discussed below and are shown in the Fig. 1.

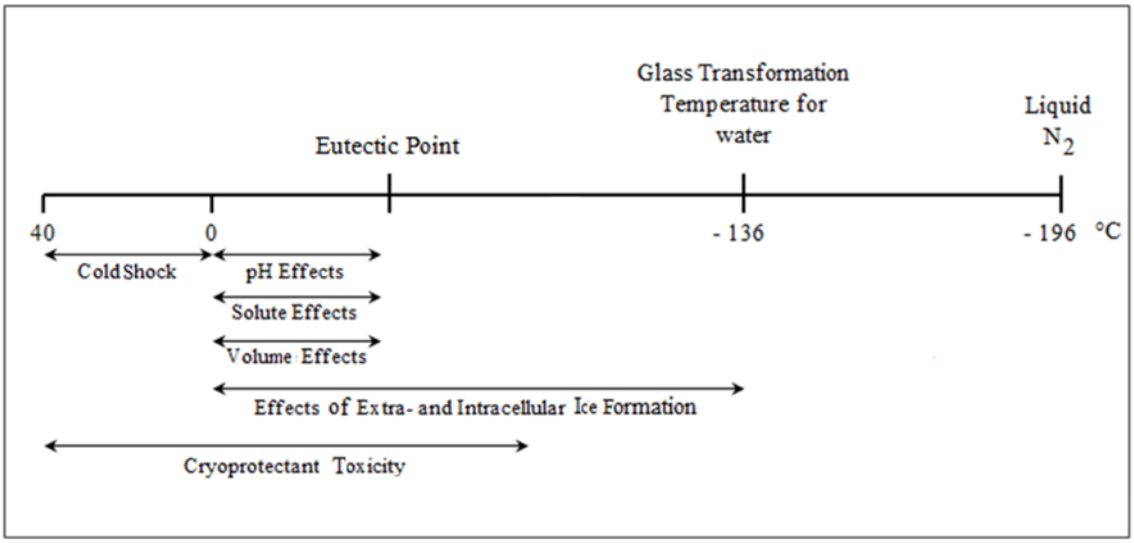

Fig. 1. Possible cryoinjuries at different temperature ranges (modified from (Jamieson, 1991)).

Chilling injury and cold shock

These are the very first damages the cell may get already during initial chilling. Chilling injury occurs following slow cooling between around +15 and -5 °C (Vajta et al., 2011) and develops over a period of time (hours) and is associated with a loss of selective permeability of the membrane (Morris, 2015).

Cold shock occurs at rapid cooling at temperature above 0 °C. Damage in sperm cells may be manifested by loss of flagellar activity, damage to intracellular organelles, and leakage of solutes via cell membranes. In particular, the loss of potassium and influx of calcium ions are associated with cold shock damage. It may happen as a result of increasing permeability of the membrane bilayer caused by phase transitions when lipid molecules are reorganized during the change from the liquid to the gel phase. Injury caused by phase separation has irreversible nature, which explains, at least in part, why cold shocked cells do not recover upon warming (Drobnis et al., 1993). According to Holt (2000), phase transitions might be involved in the cryoinjury also during the rewarming of cells.

The cell is cooled then below 0 degrees. Here the most critical is the temperature range between 0 and -40 °C as most cryoinjuries occur during pre-freezing and post-thawing over this range (Jamieson, 1991).

pH effects

Water composes some 60 to 85 % of cells (Fuller et al., 2004). Concurrently 10 % of total water is unfreezable because it is bound to macromolecules like complex mixtures of proteins, nucleic acids, lipids, and other cell constituents. As the membrane of cell is semi-permeable, free water tends to move across the cell membrane to maintain an equal concentration of solutes inside and outside the cell (Agarwal, 2011).

During cooling, the water will crystallize resulting in appearance of hyper-concentrated solutions. At the temperature of eutectic point the concentration of the solute reaches its maximum. The eutectic points of most salts are different and range approximately from 0 to -55 °C. Freezing and thawing within this temperature range will exclude the buffering capacity of these salts and, therefore, significantly change the pH of the biological solution. Fluctuations of pH may be caused not only by freezing (Berg and Dyson, 1959), but in some cases by addition of cryoprotectants (Berg and Soliman, 1969). Denaturation of proteins takes place when their pH tolerance limits are exceeded (Jamieson, 1991).

Intracellular ice effects

There are two points of view on damaging effects of intracellular ice. According to the first one, the likelihood of the formation of intracellular ice increases with the increase of cooling rate. Intracellular ice also can appear following thawing. The degree of injury is proportional to the size of the ice crystals. Small ice crystals produced during rapid freezing may not be detrimental, but the recrystallization of these small crystals, inside and outside the cell, may result in appearance of large ice crystals which mechanically destruct membrane structure (Fujikawa, 1978). However, more recent point of view is that intracellular ice formation is completely cell destroying event and cell vitrification is the only chance for cell to survive freezing and thawing processes (Katkov et al., 2012).

Extracellular ice effects

Mechanical damage of membrane by extracellular ice formation takes place when the cooling rate is very small (Fujikawa and Miura, 1986). It is possible that cell injury

will be caused by physical forces which arise when the ice field expands and constraints the area that can be occupied by the cells. Extracellular ice is usually considered not to be detrimental to most biological specimens frozen at conventional cooling rates.

Solute effects

As water is frozen out during freezing, both extra- and intracellular solutions become progressively more concentrated. These concentrated solutions can cause denaturing and osmotic effects on the membrane macromolecules (Lovelock, 1957). Membrane damage increases with time of exposure, so during slow freezing solute effects may lead to the cell death (Jamieson, 1991).

Volume effects

Occurrence of cryoinjury through volume effects is not yet fully established. It is assumed that in terms of the mechanism of freezing injury, the important point is that death of spermatozoa appears to be associated with a reduction in cell volume beyond some critical limit (Meryman et al., 1977).

Cryoprotectant toxicity

The addition of chemicals called cryoprotectants can minimize cell damage associated with ice formation or, when used at high concentrations, will suppress virtually any ice formation. Such a process is termed cryoprotection.

Cryoprotectants can suppress most cryoinjuries but, when used at higher concentrations, most of them become more and more toxic to biological materials. The most frequent side effect is a destructive change in the cell membrane (Jamieson, 1991).

All cryopreservation methods, including vitrification, involve exposure of tissues and cells to an environment that they would not normally experience and have no intrinsic genetically coded capacity to adapt (Vajta et al., 2011). Therefore, the challenge is to establish a procedure where the injuries are minimal and defensive-regenerative capacities are supported (Xin et al., 2017).

2.2.2. Cryopreservation methods

To date the two most commonly used cryopreservation approaches for animal germplasm are slow freezing and vitrification. These include quite different steps but

both are based on the same physicochemical relationships (Xin et al., 2017). The basic principles of cell cryopreservation are illustrated in Fig. 2.

Slow freezing

The first approach, i. e. slow freezing, is based on using so called optimum cooling rate, high enough not to cause the dehydration of a cell by leaving freezible water as well as to diminish the solute effect and at the same time low enough to diminish the possibility of intracellular ice crystal formation. It is possible to predict such optimum cooling rate using mathematical models (Jamieson, 1991). Only part of the freezable water leaves the cell. The remaining water vitrifies or forms small ice crystals which may be tolerable if thawing is fast enough to avoid recrystallization. The use of cryoprotectants will reduce ice growth, thus improving post-thaw survival (Jamieson, 1991).

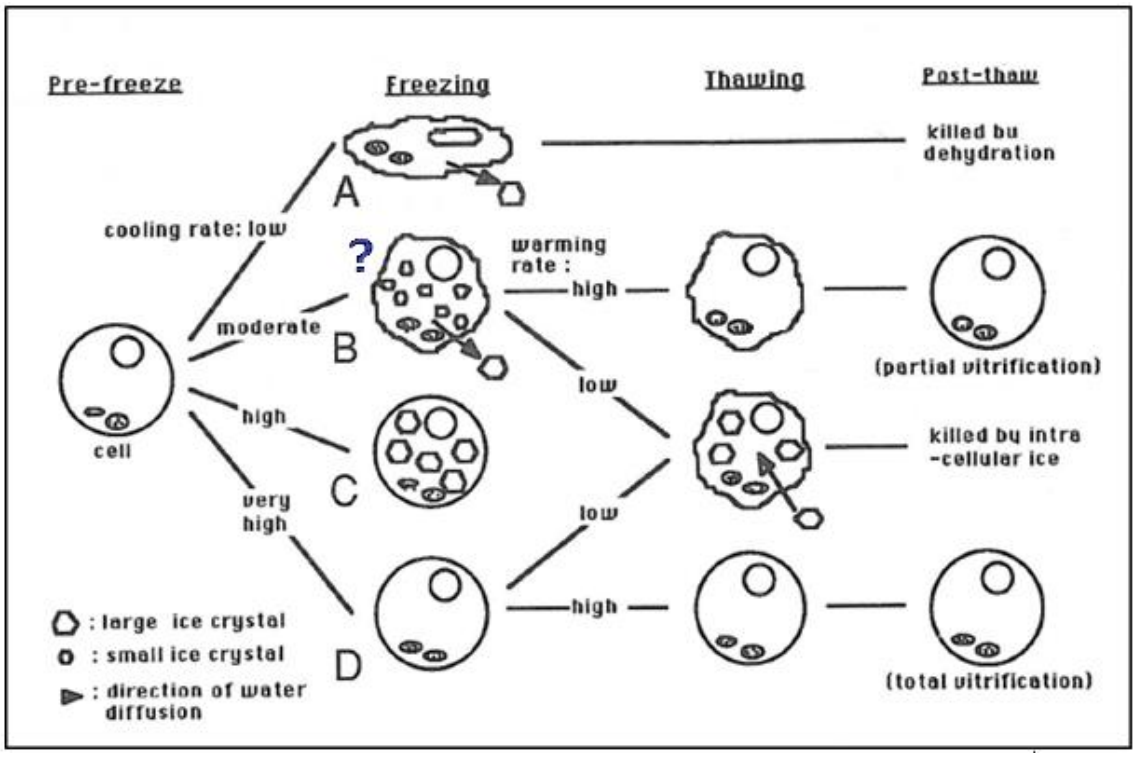

Fig. 2: Diagrammatic illustration of a cryopreservation model (modified after Jamieson, 1991). Not proved event of intracellular ice formation during "moderate" level of freezing rate is marked by "?". More detailed information is in the section "intracellular ice effects" above.

Vitrification

The second approach is vitrification. The principle of preserving cells' and tissues' structure and function by vitrification is based on virtually full prevention of both intracellular and extracellular ice formation.

Conventional vitrification methods require high cooling/warming rates, small volume of sample carriers, and using high concentrations of permeable and non-permeable cryoprotectants. These conditions cause liquids to develop into an amorphous solid state without ice formation (Xin et al., 2017).

Novel sperm vitrification methods were developed aiming to preserve fish sperm without using permeable cryoprotectants because of their toxicity and osmotic activity. However, the addition of other substances with cryoprotective activity that may have a positive effect on survival is needed. For example, low survival of rabbit sperm in case of vitrification without permeable cryoprotectants was improved by supplementation of sperm suspension with bovine serum albumin (BSA) together with sucrose or trehalose (Rosato and Iaffaldano, 2013). In other study the BSA in the concentration of 1 % was used for vitrification of rainbow trout semen (Xin et al., 2017).

To date, the method of permeable cryoprotectant-free vitrification is scarcely applied to fish semen, while classical vitrification has already been successful in cryopreservation of many fish species. At the same time the slow freezing methods are still used in most protocols.

2.2.3. Cryoprotectants

Cryoprotectants are used in the most cryopreservation protocols. Most gametes will not survive cryopreservation without cryoprotectants, which reduce cryodamage and protect them from ice formation (Moskovtsev et al., 2012; Xin et al., 2017).

Usually two types of cryoprotectants are distinguished according to their ability to penetrate the plasma membrane: permeating cryoprotectants usually of low molecular weight and non-permeating cryoprotectants, usually of high molecular weight. Dimethyl sulfoxide (Me_2SO), glycerol, ethylene glycol (EG), methanol (MeOH), and propylene glycol (PG) belong to the first group. They may increase viscosity within the cell, thereby preventing water molecules to form ice crystals (Pegg, 2007). Non-permeating cryoprotectants include sucrose, albumins, dextran, egg yolk, serum, and polyethylene

glycols. These cryoprotectants mostly prevent cellular damage caused by freeze-thaw events, like medium crystallization and recrystallization (Xin et al., 2017).

The choice of proper cryoprotectant seems to be a matter of trial-and-error in nearly all investigations; this is partly because a complete and satisfactory general explanation for the action of cryoprotectants does not exist so far (Holt, 2000). However, there is a certain correlation between the choice of a cryoprotectant and taxonomical position of selected species. Due to different sperm biology some cryoprotectants have species-specific effects on spermatozoa (Xin et al., 2017).

2.3. Taxonomy

The definition of fish is not entirely accurate, it includes different groups from hagfishes and lampreys to sharks, lungfishes and teleosts (Nelson, 2016); so it is necessary to clarify that in current thesis the term "fish" will denote a specific systematic unit, namely Actinopterygii. The subclass Actinopterygii or the ray-finned fishes is one of the major vertebrate taxa, it is not described by strong fixed character sets, but is nevertheless thought to be monophyletic.

This extremely diverse and abundant group consists of three infraclasses, 67 orders, 469 families, 4 440 genera, and about 30 500 species. It is the largest class of vertebrates extant today (Nelson, 2016).

Fishes occur in lakes, streams, estuaries, and oceans throughout the world. In most species of fishes, all individuals live entirely either in fresh or in marine waters. A small number of species belongs to the diadromous, which spend a part of their life in lakes and rivers, and a part in the oceans. Most often the purpose of reproduction serves as a cause of migration. Many freshwater and marine species are also common in brackish-water estuaries. The number of marine species prevails in actinopterygians. About 56 % of the species are known to inhabit only or almost only sea water (Nelson, 2016).

2.3.1. Importance to people

Today fishes form an important element in the economy of many nations primarily due to the fact that many species of fish are consumed as food around the world. Fish

has been an important source of protein and other nutrients for humans down the ages. Fish consumption varies by region, however, in 2013 fish accounted for about 17 % of the global population's intake of animal protein and 6.7 % of all protein consumed (FAO, 2016). Generally, an increase in fish consumption is observed at the global level. It is associated with dramatic growth in aquaculture production in the last two decades. During this period the consumption of wild fish remained almost the same (in absolute counts) while consumption of fish from aquaculture in total supply rises from 7 % in 1974 to about 50 % for today. In the year 2014 farmed sector's contribution to the supply of fish for human consumption surpassed that of wild-caught fish for the first time (FAO, 2016).

A number of modern studies have shown that a good quality fish is healthy for human organism as it is the source of vitamins, minerals, proteins and fatty acids (FAO, 2016). Fish also have recreational and psychological value to the naturalists, sports enthusiasts, and home aquarists (Nelson, 2016).

Unfortunately, the abundance and diversity of fish are in decline due to human activity. According to the International Union for Conservation of Nature and Natural Resources about 20 % of fish species are endangered or near threatened and there is no clear situation with about further 20 % of species.

It's hard to say if cryopreservation can radically change the current situation. Human detrimental effect on nature is too great. However, cryopreservation can be used as auxiliary tool among all of the other actions that must be taken to preserve these species.

2.4. Fish sperm

The structure of the fish spermatozoon is slightly simpler compared to sperm of other vertebrates. It consists from head, mid-piece and flagellum with the active inner core, called "axoneme" (Zheng and Zhang, 2012).

The structure of spermatozoa differs according to the fish belonging to certain taxonomic group and can provide useful support for identifying phylogenetic relationships. Spermatozoon structure has been already used as a taxonomic determinant in some animal groups. The remarkable book "Fish evolution and systematics: evidence

from spermatozoa" by Barrie Jamieson is devoted to the study of fish sperm with the taxonomic considerations.

Analysis of fish spermatozoa structure raised questions regarding the evolution of fish sperm, for example if it is possible that so-called "primitive" sperm is a result of secondary simplification. Such a conclusion follows from the observation that more advanced fish groups (teleosts) possess spermatozoa of simplified morphology ("primitive" type), while evolutionary ancient fishes have structurally more complicated ("advanced") spermatozoa (Jamieson, 1991).

2.4.1. Phylogenic trends in Actinopterygii rising from spermatology

The main apomorphy of the subclass Actinopterygii is shortening of the spermatozoon mid-piece, already clear in sturgeons, and typical of the secondarily simplified sperm of neopterygians. The Cladistia have biflagellate acrosomal aquasperm with prenuclear basal body that are regarded as weak autapomorphies of the Cladistia (Jamieson, 1991). The presence of three endonuclear canals and acrosome are the distinguishing apomorphies for sturgeons (Chondrostei), while distinctive feature of Neopterygii is apomorphic loss of the acrosome (Jamieson, 1991).

Each subsequent taxonomic unit has its own apomorphies. Between sperm of different taxonomical groups there are not only structural, but also physiological differences, which, in their turn, affect the success of the chosen specific cryopreservation method (Mclnnes and Norman, 1996). Extreme dissimilarities in gamete biology and structure among species are associated with evolutionary adaptation (Labbé et al., 2013).

2.4.2. Chemical and biochemical parameters of fish semen

Semen is composed of spermatozoa and seminal plasma. Many studies were published on the composition of seminal plasma in fish and much less about total sperm composition (Alavi et al., 2007). A major content of these both elements includes inorganic constituents that can determine the osmolality and pH either in seminal plasma or in spermatozoa. The composition of seminal plasma is specific and differs significantly from that of blood plasma. It contains mainly mineral compounds (sodium,

potassium, calcium, magnesium), then protein and other organic substances (in contrast to higher vertebrates in lower concentration), such as hormones and pheromones, cholesterol, glycerol, vitamins, antioxidants, free amino acids, sugars and lipids. Some components of seminal plasma can originate from damaged spermatozoa and other somatic cells such as leukocytes, and cells of the testes and spermatic ducts (Alavi et al., 2007). The main roles of seminal plasma are to create an optimal environment for the storage of spermatozoa and to support spermatozoa and physio-endocrinological function after release of sperm from the testis into the sperm duct and subsequently after discharge of sperm into the aquatic environment (Alavi et al., 2007).

Fish spermatozoa are usually immotile while being in the seminal plasma. The activating of spermatozoa motility is regulated by triggering the signal transduction systems after changes in environmental tonicity. Other external factors that influence motility of sperm in fish are pH, temperature and ion concentration (Alavi et al., 2009).

Spermatozoa of marine and freshwater species do not have specific and unique fine structural features whilst in chemical and biochemical parameters of seminal plasma there are some relationships regarding to species habitat. Thus, the highest osmolality in seminal plasma is found in marine fish. The osmolality of the seminal fluid of cyprinid fishes is usually higher in comparison to that of salmonids. Notably that the osmolality of chondrostean fish (sturgeons) seminal plasma is much lower than that of teleost fish (Alavi et al., 2007). Sperm motility is initiated by hypo-osmotic (relative to the seminal fluid) spawning environmentin freshwater fishes and by hyper-osmotic surroundings in marine fishes (Alavi et al., 2007). The model of these processes is shown in schematic Fig. 3. In some species with well developed habitat adaptations, for example tilapia (*Oreochromis mossambicus*) or medaka (*Oryzias latipes*), regulatory mechanisms of spermatozoon flagellum motility are modulated to suit the spawning environment when they are in fresh water or acclimated to sea water (Morita et al., 2006).

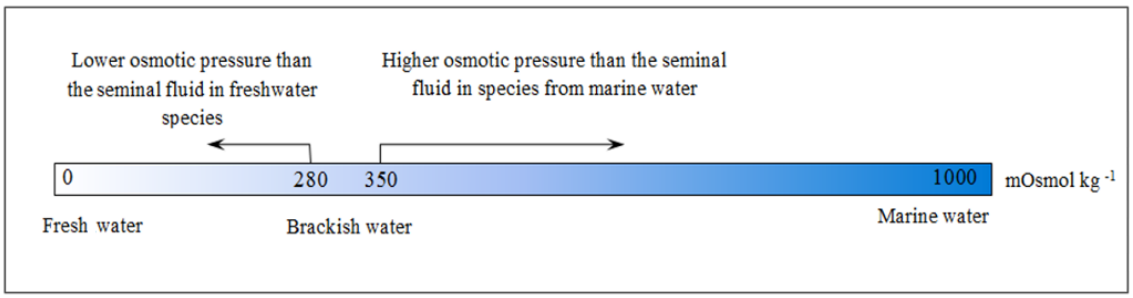

Fig. 3: Schematic model of fish sperm activation conditions occurred as a result of changes in medium osmolality. Average values 280 and 350 mOsmol kg^{-1} represent isotonic seminal fluid of some freshwater and marine fish respectively. Arrows show the direction of change in osmolality of surrounding fluid after discharge of sperm into the aquatic environment.

During the process of cryopreservation an osmolality of a sample is artificially increased by addition of some cryoprotective substances. Exposure to high cryoprotectant concentration during incubation may have negative effects on sperm physiology. This is more typical for freshwater species, that show less resistance to variations of osmolality than marine species, and the result may be an osmotic shock. Nevertheless, the presence of seminal plasma reduces the harmful effects of cryoprotectants (Magnotti et al., 2018). Motility of frozen-thawed spermatozoa and their ability to fertilize eggs are main indicators of the cryopreservation success. Understanding effects of changes in osmolality is helpful in developing optimal conditions for long-term storage of fish sperm with purpose to maintain potential sperm motility (Alavi et al., 2007).

2.5. Cryoprotocols

Typical cryoprotocol is a description of a successful cryopreservation procedure, which includes the information about cryoprotective medium composition, the rate of dilution of sample with cryoprotective medium, and details of freezing and thawing regimes. Taking into account fish taxonomic diversity and big variety of their spawning environment and feeding preferences which influence very much sperm membrane composition, the uniform protocol for different fish species was not developed yet. The

only initial steps were made in elaboration of uniform protocol (Labbe et al., 2013). The precise description of species-specific protocols is the topic of a lot of already published research papers and reviews (Labbe et al., 2013; Martínez-Páramo et al., 2017; Xin et al 2017). From these reviews it is clear that even optimization of protocols is highly required, modern studies should be performed by a standardized experimental way, which allows high repeatability of newly published results. That in turn gives additional chance for increase in effectiveness of application of existing cryoprotocols in practice of fish sperm cryobanking.

2.5.1. For how many fish species sperm do cryoprotocols exist?

For many years in a large number of studies devoted to fish sperm cryopreservation there was quoted that cryoprotocols exist for approximately 200 different species of fish. Unfortunately, this number, even being repeated from one rewiev to another, appears as not accurately estimated value and become confusing as original sources of information are not easy available nowadays. Possibly, the number of 200 fish species in which sperm was cryopreserved to the end of 20^{th} century (Zhang, 2004) was overestimated. The chronology of the appearance of information about fish species for which protocols of sperm cryopreservation were available in scientific literature can be summarized by following dates:

1953 – The first successful cryopreservation of fish sperm (Blaxter, 1953);

1995 – "To date, spermatozoa of over 50 species of freshwater and marine fish have been cryopreserved" (Rana, 1995);

1997 – "To date, over 200 reports exist for cryopreservation research in more than 65 species of fish" (Fiegel and Tiersch, 1997);

2000 – "185 reports published from 1953 to 1996 for at least 83 fish species" (Paniagua-Chávez et al., 2011; Tiersch and Mazik, 2000);

2008 – "More than 90 species and more than 200 published reports" (Tiersch, 2008).

2.5.2. Current estimate of the number of cryoprotocols

Notwithstanding hundreds of scientific papers devoted to cryoprotocols developing, the analysis of the literature data showed the absence of a unified information database on the fish species, the sperm of which was cryopreserved for today. In this regard, it became necessary to update information on this issue. To summarize a list of fish species whose semen has been cryopreserved to date, I created a table in Microsoft Excel (see Table 1 in supplements). For searching the information I used the database of the World of Science (www. webofknowledge.com), the library of USB, and other sources those are freely available on the Internet. This table consists of five columns. The first column is a scientific name and the second one is a common name of species. In some cases, there is more than one name in the Table. Occasionally I have used outdated scientific names because often these names are being changed, but in some protocols previous names are kept. Possible presence of several common names in second column comes from problems in naming itself. One fish can have different trivial names. I listed a common name as first and the most well-known names below it. The third and fourth columns contain the information about taxonomic identity and habitat conditions (water salinity) of fish. References to cryoprotocols in the last column are not definitive. They serve rather as evidence of the existence of a cryoprotocol. In the future, different parameters of these methods should be assessed and the most successful cryoprotocol for each type of fish should be identified.

Based on the data that I found, successful cryoprotocols for 233 fish species have been developed for today (Table 1 in supplements). This number is not much different from the one already quoted in several reviews, despite the fact that almost 20 years have passed since the first mention of 200 cryoprotocols published for fish sperm cryopreservation. It is clear that this branch of science is constantly evolving and according to Martínez-Páramo et al. (2017) in the last five years the publications dedicated to development of protocols still prevailed in fish sperm cryopreservation research.

2.5.3. Cryopreservation of sperm in freshwater and marine fish species

Fishes inhabit waters with different conditions throughout the world. During the data processing I took into account the habitat of fish relative to water salinity, because

the choice of cryopreservation method is closely related to biology of sperm, which, in turn, is closely linked to habitat and taxonomic position of a particular species. An ability to withstand freezing is dependent on this factor. I divided fish species into five groups on this basis (Fig. 4). As a source of information about habitat a global species database FishBase was used.

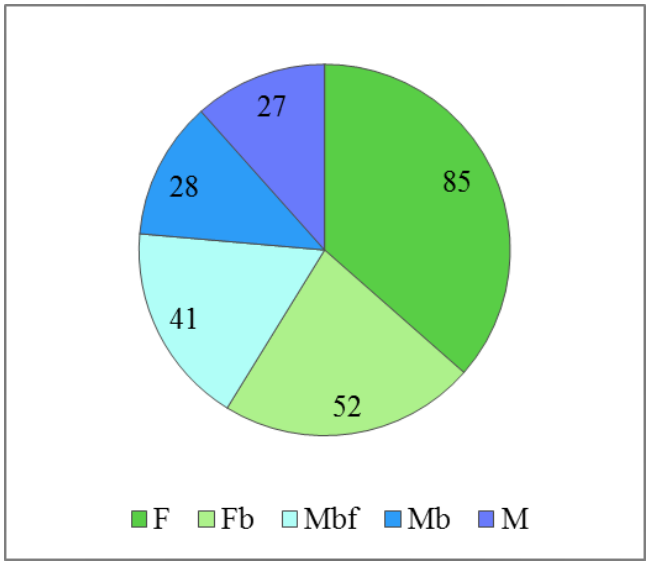

Fig. 4: The quantity of fish species for which sperm was cryopreserved with regard to their habitats (number denotes the quantity of species).
Abbreviations for habitat: F - fresh water; Fb - fresh water and brackish water; Mbf - marine, brackish, and fresh water; Mb - marine and brackish water; M - marine water.

Among species for which freezing-thawing methods are available, freshwater species and freshwater species with a tolerance to saline water make about 60 % of total number; 16 % account for diadromous species and about 24 % for species that occur in marine and brackish waters.

Generally, it is believed that salinity of spawning environment and spawning temperatures are closely related to sperm membrane composition, which in turn can determine sperm cryoresistance (Drokin, 1993; Labbe and Maisse, 1996). In the same time, the progress in sperm cryopreservation in both marine and fresh water fishes demonstrates that areal salinity is not the crucial factor for success in fish sperm cryopreservation.

2.5.4. Cryopreservation of sperm from different fish orders

In current bachelor work it was estimated that successful cryopreservation of fish spermatozoa was achieved among members of 22 orders. I used time-calibrated “fish tree of life” that highlights the evolutionary relationships of major groups (ordinal or supraordinal taxa) developed by Ricardo Betancur-R et al. (2017) to visualize the evolutionary relationships between orders for whose members sperm was successfully cryopreserved (Fig. 5). From this figure it is visible that these groups are not randomly scattered across phylogenetic tree, but are located rather close to one another according to their taxonomic relationship. Perhaps this relation can be a consequence of a similar fish biology and commercial importance which impacted the elaboration of cryopreservation method among the groups. It is noted that these orders represent about 33% of extant fish orders and quite probably the more attention should be payed to develop protocols for representatives of not studied yet orders.

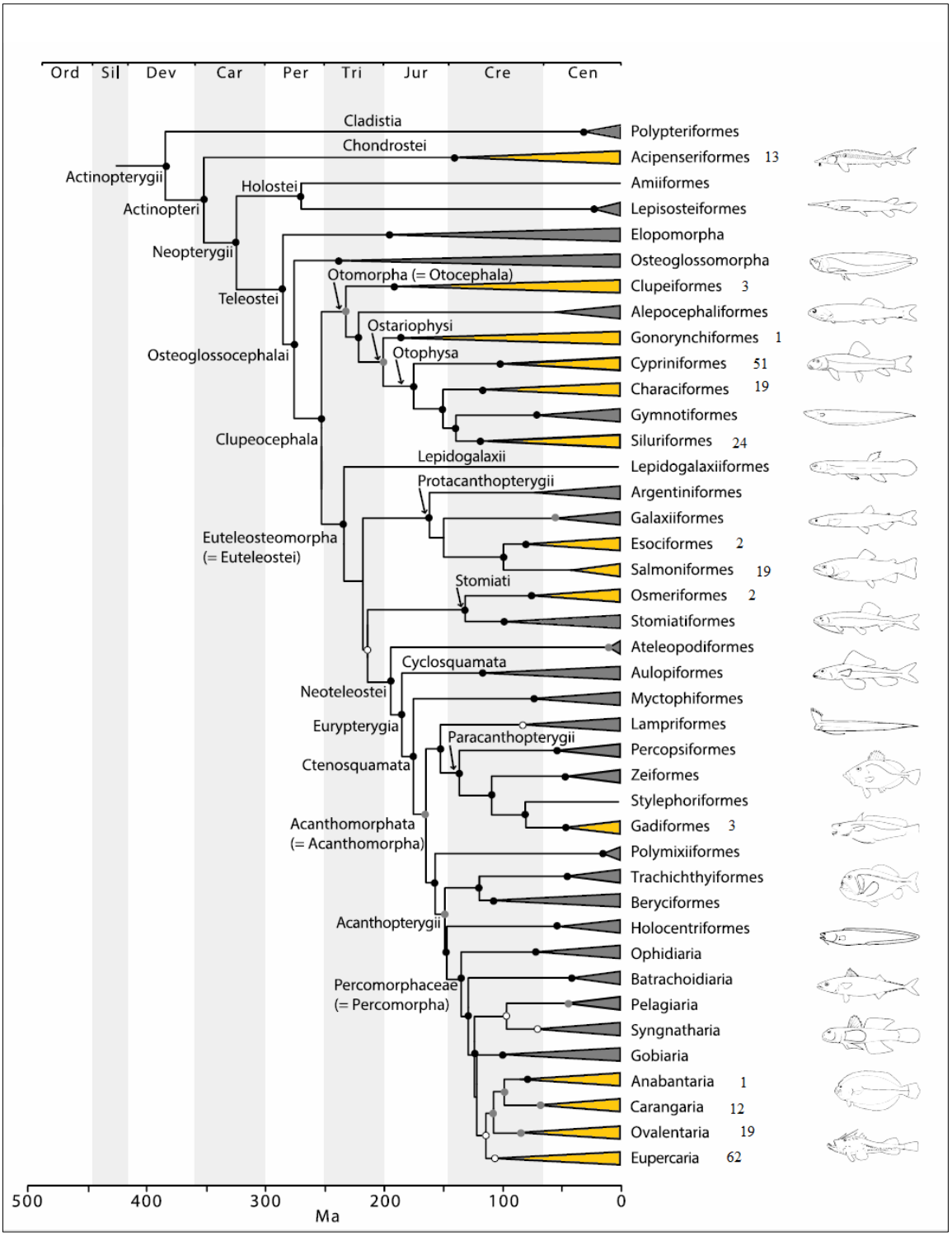

Fig. 5. Taxonomical groups for members of which sperm cryopreservation protocols are available to the date. These groups are highlighted by a yellow triangle and on the right side the numbers represent the amount of species, for which the cryopreservation protocols are described. (Modified version of Fish Tree of Life from Betancur-R et al., 2017).

3. Conclusions

In this work a review of the current state of fish sperm cryopreservation in relation to conservation measures and aquaculture practice with special focus on taxonomical position of involved species was made.

Cryopreservation is considered as an important component of effective strategy to save endangered species and also as unique tool that can be used in the aquaculture industry to preserve the genomes of domesticated species over many steps of genetic selection, and to facilitate broodstock management by extending or delaying offspring production.

Generally, compacted fish spermatozoa with a reduced cytoplasmic compartment show good tolerance to freezing if most cryoinjury factors were diminished during cryopreservation. Complication is, that due to different morphology and biology of gametes among species, single universal cryopreservation protocol cannot be offered so far. However, similar cryopreservation methods can be applied with greater success to fish belonging to taxonomically-related groups. Consequently, knowledge of the taxonomic position of the fish can provide substantive support for the development of new cryoprotocol.

Analysis of taxonomical position shows that the highest number of fish species, the sperm of which was cryopreserved, belong to the order Perciformes, followed by Cypriniformes, then Siluriformes, Characiformes, Salmoniformes and Cyprinodontiformes. Fish from the remaining orders represent about 12 % of total value. Orders, containing the species in which sperm was cryopreserved, make up almost 33 % of the total number of fish orders. It can also be noted that sperm cryopreservation was primarily used in commercially important and in less extent in endangered fish species.

This bachelor's work provides the most modern review of fish species in which sperm was cryopreserved and these data may serve as a bibliographic source for further research in fish sperm cryobiology.

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5. Supplements

Table 1. List of fish species with successfully developed protocols for sperm cryopreservation.

Scientific name	Common name	Order	Habitat	References
Abramis brama	freshwater bream	Cypriniformes	f b*	Urbanyi et al. (2006) Glogowski et al. (1999) Glogowski et al. (1997)
Acanthopagrus australis	yellowfin bream	Perciformes	m b	Thorogood and Blackshaw (1992)
Acanthopagrus latus	yellowfin seabream	Perciformes	m b f	Gwo (1994)
Acanthopagrus schlegelii	black sea bream, blackhead seabream	Perciformes	m b	Hsu et al. (2008) Lim (1998) Chao et al. (1986)
Acipenser baerii	Siberian sturgeon	Acipenseriformes	f b	Judycka et al. (2015)Sieczyński et al. (2015) Urbányi et al. (2004)
Acipenser brevirostrum	shortnose sturgeon	Acipenseriformes	m b f	Horváth et al. (2005)
Acipenser fulvescens	lake sturgeon	Acipenseriformes	f b	Ciereszko et al. (1996)
Acipenser gueldenstaedtii	Russian sturgeon, diamond sturgeon	Acipenseriformes	m b f	Yamaner et al. (2015) Huang et al. (2014) alimi et al. (2014)
Acipenser mikadoi	Sakhalin sturgeon	Acipenseriformes	m b f	Kopeika and Shilin (1993)
Acipenser persicus	Persian sturgeon	Acipenseriformes	m b f	Aramli et al. (2016) Keivanloo and Sudagar (2016) Aramli et al. (2016) Shaluei et al. (2015) Rahimi et al. (2014) Abed-Elmdoust et al. (2014) Alavi et al. (2012)
Acipenser ruthenus	sterlet	Acipenseriformes	f b	Boryshpolets et al. (2011) Lahnsteiner et al. (2004) Billard et al. (2004) Urbányi et al. (2004) Jähnichen et al. (1999)
Acipenser sinensis	Chinese sturgeon	Acipenseriformes	m b f	Liu et al. (2006)

Table 1 (continued)

Acipenser stellatus	starry sturgeon, stellate sturgeon	Acipenseriformes	m b f	Sadeghi et al. 2013
Acipenser sturio	Atlantic sturgeon	Acipenseriformes	m b f	Urbányi et al. (2004)
Alburnus chalcoides	Danube bleak	Cypriniformes	f b	Lahnsteiner et al. (2000)
Anarhichas lupus	Atlantic wolffish	Perciformes	m	François et al. (2007)
Anarhichas minor	spotted wolffish	Perciformes	m	Gunnarsson et al. (2008) François et al. (2007)
Anguilla anguilla	European eel	Anguilliformes	m b f	Herranz-Jusdado et al. (2018) ...
Anguilla japonica	Japanese eel	Anguilliformes	m b f	Koh et al. (2017) Kása et al. (2017) …
Anoplopoma fimbria	sablefish	Scorpaeniformes	m	Kása et al. (2017) Immerman and Goetz (2014) Sanchez-Serrano et al. (2014)
Arabibarbus grypus	shabout	Cypriniformes	f	Al-Mohammedi et al. (2018) Doğu (2012)
Argyrosomus regius	meagre, croaker	Perciformes	m b	Santos et al. (2018)
Aspius aspius	asp	Cypriniformes	f b	Babiak et al. (1998)
Ataeniobius toweri	bluetail goodea	Cyprinodontiformes	f	Liu et al. (2018)
Barbus barbus	barbel	Cypriniformes	f	Urbanyi et al. (2006) Lahnsteiner et al. (2000)
Barbus gonionotus	silver barb	Cypriniformes	f	Sarder et al. (2013)
Blicca bjoerkna	white bream, silver bream	Cypriniformes	f b	Urbanyi et al. (2006)
Brachymystax lenok	lenok	Salmoniformes	f	Lee and Yoshizaki (2016)
Brycinus imberi	spot-tail	Characiformes	f	Steyn end Vanvuren (1991)
Brycon amazonicus	yamu	Characiformes	f	Viveiros and Godinho (2008) Velasco-Santamaría et al. (2006) Cruz-Casallas et al. (2004)

Table 1 (continued)

Brycon henni	Brycon henni	Characiformes	f	Pineda-Santis et al. (2015) Pineda-Santis and Gómez-Oquendo (2005)
Brycon insignis	Tiete tetra	Characiformes	f	Viveiros and Godinho (2008) Viveiros et al. (2010) Viveiros et al. (2012)
Brycon moorei	Dorada	Characiformes	f	García (2018)
Brycon opalinus	pirapitinga-do-sul	Characiformes	f	Orfão et al. (2011) Viveiros et al. (2012)
Brycon orbignyanus	piracanjuba	Characiformes	f	Carolsfeld et al. (2003) Maria et al. (2006) Nascimento et al. (2012) Andrade et al. (2014) Viveiros and Godinho (2008)
Brycon orthothaenia	Brycon orthothaenia	Characiformes	f	Viveiros and Godinho (2008)
Capoeta capoeta	Seven khramulya	Cypriniformes	f	Ji et al. (2008)
Capoeta trutta	longspine scraper	Cypriniformes	f	Şahinöz et al. (2018)
Carassius auratus	goldfish	Cypriniformes	f b	Kutluyer et al. (2016)
Centropomus parallelus	fat snook	Perciformes	m b f	Tiba et al. (2009) Ferraz et al. (2013)
Centropomus undecimalis	common snook	Perciformes	m b f	Ferraz et al. (2013) Tiersch et al. (2004)
Centropristis striata	black sea bass	Perciformes	m	DeGraaf et al. (2004) Liu et al. (2013)
Channa punctatus	spotted snakehead	Perciformes	f b	Sumathi (2004)
Channa striata	striped snakehead	Perciformes	f b	Sumathi (2004)
Chanos chanos	milkfish	Gonorynchiformes	m b f	Hara et al. (1982)
Chondrostoma nasus	common nase	Cypriniformes	f	Lahnsteiner et al. (2000)
Cirrhinus cirrhosus	mrigal carp	Cypriniformes	f b	Sarder et al. (2009)
Cirrhinus mrigala	Cirrhinus mrigala	Cypriniformes	f	Betsy and Kumar (2015) Das et al. (2010)
Cirrhinus reba	Reba carp	Cypriniformes	f	Sultana et al. (2017)
Clarias batrachus	walking catfish	Siluriformes	f b	Lal et al. (2009)

Table 1 (continued)

Clarias gariepinus	African catfish	Siluriformes	f	Steyn et al. (1985) Vanderwalt et al. (1993) Urbány et al. (1999) Urbanyi et al. (1999) Horvath and Urbanyi (2000) Viveiros et al. (2000) Muchlisin et al. (2015)
Clarias macrocephalus	broadhead catfish, bighead catfish	Siluriformes	f b	Chairak (1996)
Clupea harengus	Atlantic herring and Baltic herring	Clupeiformes	m b	Blaxter et al. (1953) Rosenthal et al. (1978)
Clupea pallasii pallasii	Pacific herring	Clupeiformes	m b f	Pillai et al. (1994)
Colossoma macropomum	tambaqui, black pacu, cachama	Characiformes	f	Garcia et al. (2015) Melo-Maciel et al. (2015) Varela Junior et al. (2015) Maria et al. (2015) Carneiro et al. (2012) Oliveira et al. (2016) Júlia Trugilio Lopes et al. (2018)
Coregonus lavaretus	whitefish	Salmoniformes	f b	Ciereszko et al. (2013) Dietrich et al. (2016) Sarosiek et al. (2015) Judycka et al. (2018) Ciereszko et al. (2008)
Coregonus muksun	muksun	Salmoniformes	m b f	Piironen (1987) Piironen and Hyvarinen (1983)
Cromileptes altivelis	humpback grouper	Perciformes	m	Sean-in et al. (2009)
Ctenopharyngodon idella	grass carp	Cypriniformes	f b	Withler (1982) Lahnsteiner et al. (2000) Bozkurt et al. (2009) Bozkurt and Ogretmen (2012)
Cyclopterus lumpus	lumpfish, lumpsucker	Scorpaeniformes	m	Nordberg et al. (2015)
Cynoscion nebulosus	spotted seatrout	Perciformes	m b	Wayman et al. (1996)
Cyprinus carpio	common carp	Cypriniformes	f b	Withler (1982) Várkonyi et al. (2018) Yavaş et al. (2013) Akcay et al. (2004) ...

Table 1 (continued)

Danio rerio	zebrafish	Cypriniformes	f	Yang and Tiersch (2009) Matthews et al. (2018) ...
Dentex tumifrons	yellowback seabream	Perciformes	m	Kurokura et al. (1986) Kumai et al. (1998)
Dicentrarchus labrax	European bass	Perciformes	m b f	Martínez-Páramo et al. (2013) Peñaranda et al. (2008) Fauvel (1998)
Diplodus puntazzo	sharpsnout sea bream	Perciformes	m b	Taddei et al. (2001)
Epinephelus akaara	Hong Kong grouper	Perciformes	m	He et al. (2011) Ahn et al. (2018)
Epinephelus bruneus	longtooth grouper	Perciformes	m	Lim and Le (2013) Liu et al. (2016)
Epinephelus coioides	orange-spotted grouper	Perciformes	m b	Peatpisut and Bart (2010) Liu et al. (2016)
Epinephelus lanceolatus	giant grouper	Perciformes	m b	Tian et al. (2015) Chen et al. (2018) Kiriyakit et al. (2011) Fan et al. (2013)
Epinephelus malabaricus	Malabar grouper	Perciformes	m b	Gwo (1993)
Epinephelus marginatus	dusky grouper	Perciformes	m	Cabrita et al. (2009) Riesco et al. (2016)
Epinephelus septemfasciatus	convict grouper	Perciformes	m	Koh et al. (2010) Tian et al. (2013) Koh et al. (2011)
Epinephelus tauvina	greasy grouper	Perciformes	m	Withler and Lim (1982)
Esox lucius	northern pike	Esociformes	f b	Babiak et al. (1995) Lahnsteiner et al. (1998) Babiak et al. (1999) Zhang et al. (2010) Dietrich et al. (2016)
Esox masquinongy	muskellunge	Esociformes	f	Lin et al. (1996) Glogowski et al. (1999)
Gadus morhua	Atlantic cod	Gadiformes	m b	Rideout et al. (2004) Butts et al. (2010) Butts et al. (2011)
Gnathopogon caerulescens	Gnathopogon caerulescens	Cypriniformes	f	Higaki et al. (2017)
Goodea atripinni	blackfin goodea	Cyprinodontiformes	f	Liu et al. (2018)
Gymnocypris przewalskii	Przewalskii's naked carp	Cypriniformes	f	Wei et al. (2018)

Table 1 (continued)

Hemibagrus nemurus	bagrid catfish	Siluriformes	f b	Muchlisin et al. (2004) Chew and Zulkafli (2012) Ratanatrivong et al. (2011) Ratanatrivong et al. (1994)
Heterobranchus longifilis	vundu, sampa	Siluriformes	f	Otémé et al. (1996)
Heteropneustes fossilis	stinging catfish	Siluriformes	f b	Sumathi (2004)
Hippoglossus hippoglossus	Atlantic halibut	Pleuronectiformes	m	Ding et al. (2012) Ding et al. (2011) Babiak et al. (2008)
Hucho hucho	huchen, European huchen	Salmoniformes	f	Lahnsteiner et al. (1996) Nynca et al. (2015)
Huso huso	beluga European sturgeon	Acipenseriformes	m b f	Aramli et al. (2015) ...
Hydrocynus forskahlii	elongate tigerfish	Characiformes	f	Steyn and Vanvuren (1991)
Hypophtalmichthys molitrix	silver carp	Cypriniformes	f b	Lahnsteiner et al. (2000)
Hypophthalmichthys nobilis	bighead carp	Cypriniformes	f b	Withler (1982)
Hypsibarbus wetmorei	golden belly barb	Cypriniformes	f	Chew and Zulkafli (2012)
Ictalurus furcatus	blue catfish	Siluriformes	f b	Lang et al. (2003)
Ictalurus punctatus	channel catfish	Siluriformes	f	Christensen and Tiersch (1997) Tiersch et al. (1994) ...
Labeo calbasu	orangefin labeo	Cypriniformes	f b	Nahiduzzaman et al. (2012)
Labeo catla	catla	Cypriniformes	f b	Das et al. (2010)
Labeo rohita	roho labeo	Cypriniformes	f b	Sarder et al. (2013) Das et al. (2010) Withler (1982)
Larimichthys crocea	large yellow croaker	Perciformes	m b	Lin and You (2002) Jiang et al. (2011) Xu et al. (2014)
Larimichthys polyactis	yellow croaker	Perciformes	m	Le et al. (2011)
Lateolabrax japonicus	Japanese seabass	Perciformes	m b f	Ji et al. (2004) Gwo (2010)
Lates calcarifer	barramundi	Perciformes	m b f	Leung (1987) Palmer et al. (1993)
Latris lineata	striped trumpeter	Perciformes	m	Ritar and Campet (2000) Ritar (1999)

Table 1 (continued)

Leiarius marmoratus	Amazonian catfish	Siluriformes	f	Gheller et al. (2019)
Lepomis macrochirus	coppernose bluegill	Perciformes	f	Bates et al. (2005)
Leporinus macrocephalus	piau-acu'	Characiformes	f	Ribeiro et al. (2003) Viveiros and Godinho (2008)
Limanda ferruginea	yellowtail flounder	Pleuronectiformes	m b f	Richardson et al. (1999) Richardson et al. (1995)
Leuciscus idus	ide	Cypriniformes	f b	Bernáth et al. (2018)
Lota lota	burbot	Gadiformes	f b	Lahnsteiner et al. (2002)
Lutjanus analis	mutton snapper	Perciformes	m b	Sanches et al. (2013)
Lutjanus synagris	lane snapper	Perciformes	m	Gaitán-Espitia et al. (2013) Gaitán-Espitia et al. (2013) Sanches (2015)
Maccullochella peelii	Murray cod	Perciformes	f	Daly et al. (2008)
Makaira indica	black marlin	Perciformes	m	van der Straten et al. (2006)
Mastacembelus armatus	zig-zag eel	Synbranchiformes	f b	Rahman et al. (2016)
Megaleporinus obtusidens	piapara	Characiformes	f	Carolsfeld et al. (2003) Viveiros and Godinho (2008) Taitson et al. (2008) Caser et al. (1987)
Melanogrammus aeglefinus	haddock	Gadiformes	m	Rideout et al. (2004) Rideout et al. (2004)
Micropogonias undulatu(s)	Atlantic croaker	Perciformes	m b	Gwo et al. (1991) Gwo and Arnold (1992)
Misgurnus anguillicaudatus	pond loach	Cypriniformes	f b	Yasui et al. (2009) Yasui et al. (2012)
Misgurnus fossilis	European weatherfish	Cypriniformes	f b	Kopeika et al. (2003)
Morone saxatilis	striped bass	Perciformes	m b f	Jenkins-Keeran and Woods (2002) He and Woods (2003) He and Woods (2004) Thirumala et al. (2006)
Mugil cephalus	grey mullet	Mugiliformes	m b f	Balamurugan and Munuswamy (2017)
Mystus cavasius	Gangetic mystus	Siluriformes	f b	Islam et al. (2017)
Nandus nandus	Gangetic leaffish	Perciformes	f b	Sarder et al. (2012)

Table 1 (continued)

Nibea albiflora	yellow drum	Perciformes	m	Dai et al. (2012)
Odontesthes bonariensis	prejerrey, Argentinian silverside	Atheriniformes	m b f	Renard et al. (1994) Lichtenstein et al. (2010) Alves et al. (2016)
Ompok pabda	pabda catfish	Siluriformes	f	Sarder et al. (2013)
Oncorhynchus masou formosanus	Formosan landlocked salmon	Salmoniformes	f	Gwo et al. (1999)
Oncorhynchus masou ishikawae	amago salmon	Salmoniformes	m b f	Ohta et al. (1995)
Oncorhynchus masou masou	mason salmon, cherry salmon	Salmoniformes	m b f	Lim et al. (2008) Ohta et al. (1995)
Oncorhynchus mykiss	rainbow trout	Salmoniformes	m b f	Holtz (1993) Ninhaus-Silveira (2006) Tekin et al. (2003) Merino et al. (2011) Ciereszko et al. (2014) Cabrita et al. (2001) Nynca et al. (2017) Judycka et al. (2019) ...
Onychostoma barbatulum	Taiwan shovel-jaw carp	Cypriniformes	f	Tsai et al. (2009)
Oreochromis mossambicus	Mozambique tilapia, black tilapia	Cichliformes	f b	Harvey (1983) Ugwu et al. (2019) ...
Oreochromis niloticus	Nile tilapia	Cichliformes	f b	Godinho et al. (2003) Yong et al. (2018)
Oreochromis spp.	Thailand tilapia	Cichliformes	f	Navarro et al. (2014)
Oryzias latipes	medaka, Japanese rice fish	Beloniformes	f b	Krone and Wittbrodt (1997) Aoki et al. (1997) Yang and Tiersch (2009) Yang et al. (2010)
Osmerus mordax	rainbow smelt	Osmeriformes	m b f	DeGraaf and Berlinsky (2004)
Pagrus major	red seabream	Perciformes	m	Liu et al. (2014) Liu et al. (2010) Xiao et al. (2008) Liu et al. (2006) ...
Pangasianodon gigas	Mekong giant catfish	Siluriformes	f	Ana Viveiros (2011)
Pangasius bocourti	basa, Mekong catfish	Siluriformes	f	Kainin et al. (2012)
Pangasius hypophthalmus	striped catfish, iridescent shark	Siluriformes	f	Kwantong and Bart (2003) Withler (1982) Umaa Rani et al. (2014)

Table 1 (continued)

Pangasius larnaudii	spot pangasius	Siluriformes	f	Kwantong and Bart (2006)
Pangasius nasutus	Pangasiid catfish	Siluriformes	f	Chew and Zulkafli (2012)
Parahucho perryi	Sakhalin taimen	Salmoniformes	m b f	Kusuda et al. (2005)
Paralichthys adspersus	fine flounder	Pleuronectiformes	m	Catcoparco et al. (2012)
Paralichthys dentatus	summer lounder	Pleuronectiformes	m b	Brown et al. (2012)
Paralichthys lethostigma	southern flounder	Pleuronectiformes	m b	Hu et al. (2016) Cuevas-Uribe et al. (2017)
Paralichthys olivaceus	bastard halibut, olive flounder	Pleuronectiformes	m	Zhang et al. (2003) Tabata and Mizuta (1997)
Paralichthys orbignyanus	Brazilian flounder	Pleuronectiformes	m b	Lanes et al. (2008)
Perca flavescens	yellow perch	Perciformes	f b	Ciereszko et al. (1993) Glogowski et al. (1999) Miller et al. (2018)
Perca fluviatilis	European perch	Perciformes	f b	Judycka et al. (2018) Kása et al. (2017) Bernáth et al. (2015) Rodina et al. (2008)
Piaractus brachypomus	pirapitinga	Characiformes	f	Viveiros and Godinho (2008) Oliveira et al. (2007) Viveiros et al. (2011) Oliveira et al. (2007) Nascimento et al. (2010) Ramirez-Merlano et al. (2011)
Piaractus mesopotamicus	pacu	Characiformes	f	Carolsfeld et al. (2003) Paulino et al. (2012) Pires et al. (2018) Galo et al. (2018) Andrade et al. (2014)
Plagiognathops microlepis	smallscale yellowfin	Cypriniformes	f	Du et al. (2018)
Planiliza haematocheila	so-iuy mullet	Mugiliformes	m b f	Dzuba and Kopeika (1997)
Plecoglossus altivelis	ayu sweetfish	Osmeriformes	m b f	Yokoi et al. (2009) Yokoi et al. (2009)
Pleuronectes platessa	European plaice	Pleuronectiformes	m b	Pullin (1972)
Poecilia reticulata	guppy	Cyprinodontiformes	f b	Huang et al. (2009)
Poecilia sphenops	black molly	Cyprinodontiformes	f b	Huang (2009)

Table 1 (continued)

Pogonias cromis	black drum	Perciformes	m b	Wayman et al. (1997)
Polyodon spathula	paddlefish	Acipenseriformes	f	Brown and Mims (1999) Horváth et al. (2006) Horváth et al. (2010)
Pomoxis annularis	white crappie	Perciformes	f	Culpepper et al. (2017)
Probarbus jullieni	Isok barb	Cypriniformes	f b	Chew et al. (2010) Chew and Zulkafli (2012)
Prochilodus argenteus	prochilodus argenteus	Characiformes	f	Viveiros and Godinho (2008)
Prochilodus brevis	Brazilian bocachico	Characiformes	f	Nunes et al. (2016) Pinheiro et al. (2016) do Nascimento et al. (2017) Pinheiro et al. (2014)
Prochilodus lineatus	streaked prochilod, curimba	Characiformes	f	Murgas et al. (2007) Viveiros and Godinho (2008) Carolsfeld (2003) Andrade et al. (2004) Coser et al. (1984)
Prochilodus magdalenae	bocachico	Characiformes	f	Martinez et al. (2012) Atencio et al. (2013) ...
Psammoperca waigiensis	Waigieu seaperch	Perciformes	m b	Le et al. (2017)
Pseudoplatystoma corruscans	spotted sorubim	Siluriformes	f	Carolsfeld et al. (2003) Viveiros and Godinho (2008)
Pseudoplatystoma metaense	bagre rayado	Siluriformes	f	Ramirez-Merlano et al. (2011)
Pseudoplatystoma reticulatum	cachara	Siluriformes	f	Streit et al. (2015)
Pseudopleuronectes americanus	winter flounder	Pleuronectiformes	m	Rideout et al. (2003)
Ptychocheilus lucius	Colorado pikeminnow	Cypriniformes	f	Tiersch et al. (2004)
Puntius gonionotus	silver barb, Java barb	Cypriniformes	f	Routray et al. (2008) Vuthiphandchai et al. (2014) Withler (1982)
Rachycentron canadum	cobia	Perciformes	m b	Caylor et al. (1994)

Table 1 (continued)

Rhamdia quelen	South American catfish	Siluriformes	f	Viveiros and Godinho (2008) Goes et al. (2017)
Rhinogobius sp. BI	freshwater gobies	Perciformes	f	Yokoi et al. (2008)
Rhinogobius sp. CB	freshwater gobies	Perciformes	f	Yokoi et al. (2008)
Rutilus frisii kutum	Caspian sea kutum	Cypriniformes	f b	Mohammad Pourkazemi et al. (2009)
Rutilus meidingerii	-	Cypriniformes	f	Lahnsteiner et al. (2000)
Rutilus rutilus	roach	Cypriniformes	f b	Urbanyi et al. (2006)
Salminus brasiliensis	dourado	Characiformes	f	Zanandrea et al. (2016) Coser et al. (1984) Carolsfeld et al. (2003) Oliveira (2006)
Salmo macrostigma	Salmo macrostigma	Salmoniformes	m b f	Iaffaldano et al. (2015)
Salmo marmoratus	marble trout	Salmoniformes	f	Kása et al. (2018) Horváth et al. (2015)
Salmo salar	Atlantic salmon	Salmoniformes	m b f	Dziewulska et al. (2011) Gallant et al. (1993) ...
Salmo trutta f. caspius	brown trout, Caspian brown trout	Salmoniformes	m b f (f b)	Sarv et al. (2006) Moghanloo et al. (2007)
Salmo trutta f. lacustric	brown trout, lake trout	Salmoniformes	m b f	Lahnsteiner et al. (1997)
Salmo trutta m. fario	brown trout, river trout	Salmoniformes	m b f (f b)	Horváth et al. (2015) Lahnsteiner et al. (1997)
Salvelinus alpinus	Arctic char	Salmoniformes	m b f	Piironen (1993) Magyary et al. (1996) Richardson et al. (2000) Mansour et al. (2006)
Salvelinus fontinalis	brook trout	Salmoniformes	m b f	Judycka et al. (2017) Judycka et al. (2019) Lahnsteiner (2000) ...
Sander lucioperca	pikeperch, zander	Perciformes	f b	Bokor et al. (2007) Bokor et al. (2008)
Sander vitreus	walleye	Perciformes	f b	Moore (1987) Bergeron et al. (2002) Miller et al. (2018)
Sander volgensis	Volga pikeperch	Perciformes	f b	Bokor et al. (2007)

Table 1 (continued)

Scaphyrinchus albus	pallid sturgeon	Acipenseriformes	f	Horváth, et al. (2005)
Scardinius racovitzai	warm water rudd	Cypriniformes	f	Müller et al. (2018)
Sciaenops ocellatus	red drum	Perciformes	m b	Wayman et al. (1998)
Schizothorax curvifrons	Sattar snowtrout	Cypriniformes	f	Agarwal (2005)
Schizothorax esocinus	Chirruh snowtrout	Cypriniformes	f	Wani (2015)
Schizothorax progastus	Dinnawah snowtrout	Cypriniformes	f	Agarwal (2005)
Schizothorax richardsonii	snowtrout	Cypriniformes	f	Agarwal et al. (2009)
Scophthalmus maximus	turbot	Pleuronectiformes	m b	Dreanno et al. (1997) Suquet et al. (2000) Chereguini et al. (2003) Suquet et al. (1998)
Sillago ciliata	sand whiting	Perciformes	m b	Young et al. (1992)
Silurus asotus	Amur catfish	Siluriformes	f	Gil et al. (2017)
Silurus glanis	wels catfish	Siluriformes	f b	Marian and Krasznai (1985) Linhart et al. (1993) Linhart et al. (2005)
Siniperca chuatsi	mandarin fish	Centrarchiformes	f	Ding et al. (2009)
Solea senegalensis	Senegalese sole	Pleuronectiformes	m	Riesco et al. (2017)
Sparus aurata	gilt-head bream	Perciformes	m b	Chambeyron and Zohar (1990) Fabbrocini et al. (2000) Beirão et al.(2012) Tirpan et al. (2016) Zilli et al. (2018)
Squalius cephalus	common chub	Cypriniformes	f b	Lahnsteiner et al. (2000)
Steindachneridion scriptum	suruvi	Siluriformes	f	Pereira et al. (2018)
Stenodus leucichthys	sheefish	Salmoniformes	m b f	Tikhomirov et al. (2011)
Systomus sarana	olive barb	Cypriniformes	f b	Nahiduzzaman et al. (2011)
Tachysurus fulvidraco	yellow catfish, yellowhead catfish	Siluriformes	f	Yang et al. (2017) Pan et al. (2008)
Takifugu niphobles	marine puffer	Tetraodontiformes	m	Gwo et al. (1993)
Takifugu rubripes	Japanese puffer	Tetraodontiformes	m b f	Yoshikawa et al. (2018)
Tanakia limbata	oily bitterling	Cypriniformes	f	Ohta et al. (2001)

Table 1 (continued)

Thamnaconus septentrionalis	Filefish	Tetraodontiformes	m	Kang et al. (2004)
Thunnus orientalis	Pacific bluefin tuna	Perciformes	m b	Gwo et al. (2005)
Thymallus thymallus	Adriatic grayling	Salmoniformes	f b	Lahnsteiner et al. (1992) Lahnsteiner et al. (1996) Lahnsteiner et al. (1997) Lahnsteiner (2000) Nynca et al. (2015) Horváth et al. (2015) Kása et al. (2018)
Tinca tinca	tench	Cypriniformes	f b	Rodina et al. (2007) Lujić et al. (2015)
Tor douronensis	Semah mahseer	Cypriniformes	f	Chew et al. (2010)
Tor khudree	Deccan mahseer	Cypriniformes	f	Patil and Lakra (2005)
Tor putitora	Putitor mahseer	Cypriniformes	f	Patil and Lakra (2005)
Tor tambroides	Thai mahseer	Cypriniformes	f	Chew et al. (2010)
Verasper variegatus	spotted halibut	Pleuronectiformes	m	Tian et al. (2008) Liu et al. (2006)
Vimba vimba	vimba bream	Cypriniformes	f b	Lahnsteiner et al. (2000)
Xenotoca eiseni	redtail splitfin	Cyprinodontiformes	f	Liu et al. (2018) Liu et al. (2018)
Xiphophorus couchianus	Monterrey platyfish	Cyprinodontiformes	f	Huang et al. (2004) Yang et al. (2009)
Xiphophorus hellerii	green swordtail	Cyprinodontiformes	f	Cuevas-Uribe et al. (2011)
Xiphophorus maculatus	southern platyfish	Cyprinodontiformes	f	Pinisetty et al. (2005) Yang et al. (2012)
Xiphophorus variatus	variatus platy	Cyprinodontiformes	f	Yang et al. (2012) Yang and Tiersch (2009)
Xyrauchen texanus	razorback sucker	Cypriniformes	f	Tiersch et al. (1998)
Zoarces americanus	ocean pout	Perciformes	m b	Yao et al. (2000)
Total: 233 species				

* - Codes for habitat: m - marine, b - brackish-water, f - freshwater.

5.1. References for the table in supplements

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6. Abstrakt

Tato práce je věnována zkoumání současného stavu kryokonzervace spermatu ryb ve vztahu k akvakultuře a ochranným opatřením se zvláštním zaměřením na taxonomii spermií ryb.

Na základě intenzivní analýzy dostupné literatury na toto téma bylo zjištěno, že kryokonzervace je v současné době považována za jednu z důležitých složek efektivní strategie pro záchranu ohrožených druhů a také jako jedinečný nástroj, který lze využít v průmyslu akvakultury k usnadnění řízení chovů. Bylo shrnuto, že v současné době, byly s různým úspěchem kryokonzervované spermie z 233 paprskoploutvých ryb náležejících do 22 řádů, pomocí různých kryokonzervačních protokolů. Tyto údaje jsou prezentovány ve formě tabulky v příloze. Pro vytvoření této databáze byla jako základní zdroj informací použita vědecká citační služba Web of Science (Clarivate Analytics), následně doplněná knihovními zdroji. Ze získaných dat se předpokládá, že hlavní část studií byla zaměřena na ekonomicky významné druhy ryb a menší část studií byla zaměřena na ohrožené druhy ryb. Zvláště zajímavé je pozorování, že podobná metoda kryokonzervace může být aplikována s větším úspěchem u druhů ryb patřících do taxonomicky příbuzných skupin. Taxonomická diverzita ryb je spojena se specifickými morfologickými a fyziologickými vlastnostmi jejich gamet. To následně znamená, že je nutné vyvinout druhově specifické protokoly kryokonzervace spermatu pro druhy, které dosud nebyly studovány a jsou vystaveny riziku zániku. Taxonomická analýza ukazuje, že nejvyšší počet druhů ryb, jejichž spermie byly kryokonzervované, patří do řádu ostnoploutví (Perciformes), následuje máloostní (Cypriniformes), dále sumci (Siluriformes), trnobřiší (Characiformes), lososotvární (Salmoniformes) a halančíkovci (Cyprinodontiformes). Je třeba poznamenat, že tyto řády představují přibližně 33% existujících řádů ryb a nyní je zřejmé, že by měla být věnována větší pozornost vývoji protokolů pro zástupce řádů, které nejsou zapojeny do kryobiologických studií. Tato bakalářská práce poskytuje nejmodernější přehled druhů ryb, jejichž spermie byly kryokonzervovány, a tyto údaje mohou sloužit jako základ a bibliografický zdroj pro další výzkum kryobiologie rybích spermií.

Klíčová slova: Actinopterygii, rybí spermie, kryokonzervace, kryoprotokol, kryobanka, taxonomie.

7. Abstract

Current thesis is devoted to exploration of the current state of fish sperm cryopreservation in relation to aquaculture and conservation measures with special focus on fish sperm taxonomy.

Based on intensive analysis of available literature on the topic it was found that nowadays cryopreservation is considered as one of the important components of effective strategy to save endangered species and also as an unique tool that can be used in the aquaculture industry to facilitate broodstock management. It was summarized that nowadays sperm from 233 actinopterygian fishes belonging to 22 orders was cryopreserved applying different cryopreservation protocols with varying success. These data are presented in the form of a table in supplements. To create this database the scientific citation indexing service Web of Science (Clarivate Analytics) was used as the basic source of information subsequently supplemented by library sources. From the data obtained it is assumed, that the main part of studies was focused on economically important fishes and the minor part of the studies was focused on endangered fish species. Of special interest is the observation that similar cryopreservation method may be applied with greater success in fish species belonging to taxonomically-related groups. Fish taxonomical diversity is associated with specific morphological and physiological features of their gametes. That in turn entails the necessity to develop species-specific protocols of sperm cryopreservation for species not studied yet and being under risk of extinction. Taxonomical analysis shows that the highest number of fish species, the sperm of which was cryopreserved, belong to the order Perciformes, followed by Cypriniformes, then Siluriformes, Characiformes, Salmoniformes and Cyprinodontiformes. It is noted that these orders represent about 33% of extant fish orders and it is obvious now that more attention should be payed to develop protocols for representatives of orders non-involved into cryobiological studies. This bachelor's work provides the most modern review of fish species in which sperm was cryopreserved and these data may serve as a base and bibliographic source for further research in fish sperm cryobiology.

Keywords: Actinopterygii, fish sperm, cryopreservation, cryoprotocols, cryobanking, taxonomy.