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Ejaculate Allocation and Sperm Competition in Alternative Reproductive Tactics of Salmon and Trout: Implications for Aquaculture

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1. Introduction

Aquacultural production has increased globally and today most of salmon consumed in Sweden originates from hatcheries. It is predicted that aquaculture will produce more food for human consumption than capture fisheries (Anon 2009). Freshwater aquaculture contributes to 48 percent by value and mariculture contributes 36 percent by value globally. Norway and Chile are the leading nations producing farmed salmonids, accounting for 33 and 31 percents of aquacultural production (Anon 2009). A common way of salmonid propagation in hatcheries involves mixing of milt from several adult males for fertilization eggs of single or several females. Such procedure invariably involves sperm competition between milt from several males to fertilize eggs of individual females.

Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are cold water stenotherm fish species with pronounced population differences in time of gonad maturation and life history patterns. Ecological conditions and genetic liability fuel seasonal variation in the reproductive cycle dynamics. This cycle is characterized by a feed-back mechanism: gonadal development in smolt (sub-adults migrating from the nascent river to the sea) determines time of sea/lake period before fish return to freshwater spawning grounds. Northern, cold-climate populations may mature as precocially mature parr in the second year of life (Dalley et al 1983; Myers 1984), whereas southern salmonid populations were found to mature precocially already in the first year of life (Bagliniere & Maisse 1999).

Sperm competition is the competition between sperm from several males for fertilization of the female's eggs during a single reproductive cycle (Parker 1970). Since males are capable of repeated matings at a much higher rate than females, they have evolved adaptations to prevent competitor males from ejaculating with the same female, securing thereby paternity. Adaptations to competition for securing reproductive success have created alternative reproductive strategies, which are genetically based life history allocation and behavioural rules affecting the manner an individual spreads its reproduction over the lifetime (Brommer 2000). Atlantic salmon and brown trout exhibit alternative male maturation phenotypes (tactics): anadromous males and preociously mature parr males, which commonly engage in sperm competition at spawning grounds. Alternative reproductive tactics are phenotypes that are an expression of the life history strategy, selected to maximize individual reproductive success, even if this involves reduced survival. In many fish species, alternative reproductive tactics are characterized by a conspicuous difference in age and size at maturity and differ in relative investment to gonad and somatic tissue (Taborsky 1994). Difference in age and size at sexual maturity has created alternative spawning behavioural tactics that are tools for securing reproductive success, such as "guarder" behaviour by dominant males and "sneaker" behaviour by subordinates. This review looks at energy allocation strategies of the alternative mating phenotypes of Atlantic salmon and brown trout and places this selective pressure in the context of interbreeding between escaped farmed fish and their wild conspecifics. Its objective is to review the proximate mechanisms of sperm competition and its evolutionary implications in the two sympatrically occurring salmonid species exhibiting alternative male maturation tactics and connect these to increased aqua-cultural production today. Possible effects of these procedures on genetic population structure as a consequence of escaped farmed fish from aquacultural production facilities will be considered in this chapter.

2. Sperm cell

In the salmonid spermatozoon, the following parts are morphologically distinct:

1. sperm plasma membrane which is the mediator of the signals for sperm motility,
2. sperm head with a nucleus containing the haploid paternal genetic material,
3. sperm mid-piece with a circular mitochondrion, where glycogene, phospholipids and phosphocreatine are the substrates for ATP production that provides energy for sperm motility,
4. sperm flagellum with a central bundle of microtubules with a 9+2 organisational pattern, the axoneme, which is a locomotory component of the sperm cell.

2.1 Sperm membrane

Sperm plasma membrane is the semipermeable barrier that defines sperm body, about 10 nm thick (Baccetti 1985). Water surrounding the cell membrane tends to enter the cell, which would eventually cause it to burst. Freshwater fishes have evolved mechanisms to keep water outside the cytoplasm, in order to maintain cellular stability. Sperm plasma membrane functions as the main receptor of the environmental signals for motility, such as the hypotonicity in freshwater after ejaculation, which initiates sperm motility of freshwater teleosts (Morisawa and Suzuki 1980). High potassium concentrations in the seminal plasma of salmonid fishes are responsible for the inhibition of sperm motility (Stoss 1983). In contrast, changes in the external divalent cation concentrations and in osmolality initiate sperm motility concomitantly (Morisawa and Suzuki 1980). After ejaculation, potassium leaves sperm cell through ion channels hyperpolarizing thereby the cell membrane. This membrane hyperpolarization event is the trigger for the initiation of sperm motility (Morisawa 1994). Simultaneous increase in intracellular calcium levels causes activation of the enzyme adenylyl cyclase, which catalyzes the synthesis of cyclic AMP (cAMP) from ATP (Morisawa and Okuno 1982). cAMP is an intracellular signal, which activates the enzyme protein kinase, the enzyme activating tyrosine kinase with the function to phosphorylate a 15K protein (Morisawa and Hayashi 1985). Change in intracellular pH is not a primary factor for regulation of sperm motility in freshwater fishes (Morisawa et al 1999). Signal transmission traversing the sperm plasma membrane results in the cascade of events with an ultimate function to maintain the communication between a mature sperm cell and its environment.

2.2 Sperm head

Ellipsoid trout sperm head is 2,5 μm long and 1,5-2 μm in diameter, containing the cell nucleus (Billard 1983). Teleost fish spermatozoa have no acrosome at the anterior of the sperm head, a structure containing the enzymes that hydrolyse the egg envelopes, which is coupled with the presence of an orifice, the micropyle, on the teleostean egg (Ginsburg 1972). Sperm nucleus is transcriptionally inactive. The nucleoplasm of fish spermatozoa consists of nucleoprotamines, which after fertilization, when the hereditary material is activated, are substituted for histones (Figure 1).

Sperm movement ensues as the result of the viscous interactions of sperm flagella with the surrounding medium (Taylor 1951). Gray and Hancock (1955) calculated that the viscous drag of the sperm head was small relative to the viscous drag of the flagellum itself. Thus, sperm head has only a negligible effect on the sperm cell locomotion (Gray and Hancock 1955; Humphries at al. 2008).

2.3 Mid-piece

The salmon sperm middle piece is 0.30- 0.95 μm long (Vladić et al 2002). Sperm movement commences from the base of the flagellum, and is performed by sliding movements between flagellar proteins. A single ring-shaped mitochondrion surrounds the midpiece in salmonid fishes (Jamieson 1991; Figure 1). The mitochondrial function is to synthesize ATP by the process of oxidative phosphorylation from endogenous phospholipids, glycolipids and glycogene (Stoss 1983). ATP produced in the mitochondrial oxidative phosphorylation prior to ejaculation is the main energetic source for sperm motility. It is hydrolysed by the molecular motor, dynein ATPases, in the course of motlilty. An ATP molecule contains two phosphoanhydride bonds, which liberate free energy when hydrolysed to ADP or AMP. This ATP/ADP cycle is the fundamental mode of energy conversion in living systems. Atkinson (1968) proposed that the energy charge:

$$\mathrm{EC}= \frac{2(ATP)+(ADP)}{2[(ATP)+(ADP)+(AMP)]} \tag{1}$$

regulates the energy metabolism in all living systems. In salmon, sperm energy charge increased with sperm tail length (Vladić et al 2002), which agrees with the finding of greater ADP concentrations in shorter sperm cells (Vladić 2001).

In the process of energy transduction, the free energy of respiration is the driving force for ATP production by the F_1F_0 ATP synthase (Harold 1986; Kinosita et al 2000). It was suggested that trout mitochondria have a low oxidative phosphorylation capacity, as ATP stores are quickly depleted in the course of sperm motility due to hydrolysis of ATP by dynein ATPase (Christen et al. 1987). Thus, a rate of mitochondrial respiration in fish spermatozoa is insufficient to maintain endogenous ATP reserves for prolonged motility (Cosson at al. 1999). In the Atlantic salmon, length of the sperm mid-piece was positively associated with the sperm ATP concentrations confirming thereby mitochondrial origin of ATP (Vladić et al 2002).

2.4 Sperm flagellum

The salmon sperm flagellum is 35- 45 μm long (Vladić et al 2002). Sperm flagella contain a uniform microtubular structure of the axoneme, comprised of nine peripheral and two central microtubules, surrounded by the plasma membrane (Afzelius 1959). The two central tubules are comprised of single microtubules, while the nine peripheral tubules are comprised of a complete A-tubule and an incomplete B-tubule. The molecular motor enzyme complex, adenosine triphosphatase (ATPase) activity involves a "dynein", which is an ATPase protein that drives the sliding of the outer doublet microtubules in sperm flagella (Harrison & King 2000). Some dynein molecules are assembled together with other proteins into macromolecular complexes called dynein arms. The peripheral microtubules have two rows of dynein arms along the length of the principle part of the flagellum. Guanosine nucleotides instead of adenosine nucleotides as in actin were detected in an additional isolated microtubule protein, which was named "tubulin" (Mohri and Ogawa 1975). This dynein-tubulin system is the molecular motor, which drives the flagellar movement of spermatozoa (Woolley 2000). Dynein ATPase proteins are bound to the A-tubule. The dynein arms of one peripheral doublet will walk on its neighbour to produce force for the flagellar movement, under hydrolysis of ATP. Thus, the beating of sperm flagella is the result of an active sliding between adjacent doublets of the axoneme powered by the ATP-driven mechanochemical cycle (Omoto 1991; Harrison & King 2000).

A thin filament devoid of dynein arms is present at the terminal end of the sperm flagellum (Vladić et al 2002). This cell structure is an universal feature of animal spermatozoa (Retzius 1904, Franzén 1956). Length of this flagellar portion in salmon spermatozoa was 2- 4 μm and contains only the two central microtubular pair (Vladić et al 2002). Since this region of the sperm flagellum experiences an increased viscous drag relative to the rest of the sperm flagellum an improvement in sperm propulsive effectiveness as an adaptation to viscous resistances has been proposed (Omoto and Brokaw 1982). Importantly, sperm fertility was positively related to the size of the thin sperm tail end piece fillament, suggesting adaptation to the viscosity of the aquatic medium (Vladić et al 2002; Figure 2).

3. Sperm competition in salmonids

Success in sperm competition depends on behaviour of the competing males and of the contested female, as well as on the frequencies with which different behavioural tactics are played in the population: therefore sperm competition models are analysed in the framework of the evolutionary game theory (Maynard Smith 1982). These games are designed to find an "unbeatable" or evolutionary stable strategy (ESS), strategy which, after adopted by all individuals in the population, cannot be invaded by a mutant playing an alternative strategy. The game-theoretic models are phenotypic and do not include genetics of the participants (Maynard Smith 1982).

The assumptions of the sperm competition games are (sensu Parker 1998):

1. Males in competition have specified information about their physiological state, and a tactical decision is made about the behaviour that yields the highest pay-off for that individual. Indeed, phenotypic plasticity may be viewed as an individual response to its physiological state (McNamara and Houston 1996);
2. There is a range of possible ejaculation decisions that are dependent on his state, which includes resource-holding potential, fighting ability, age and size of the individual;
3. Several male ejaculates must compete for fertilization of a single egg clutch;

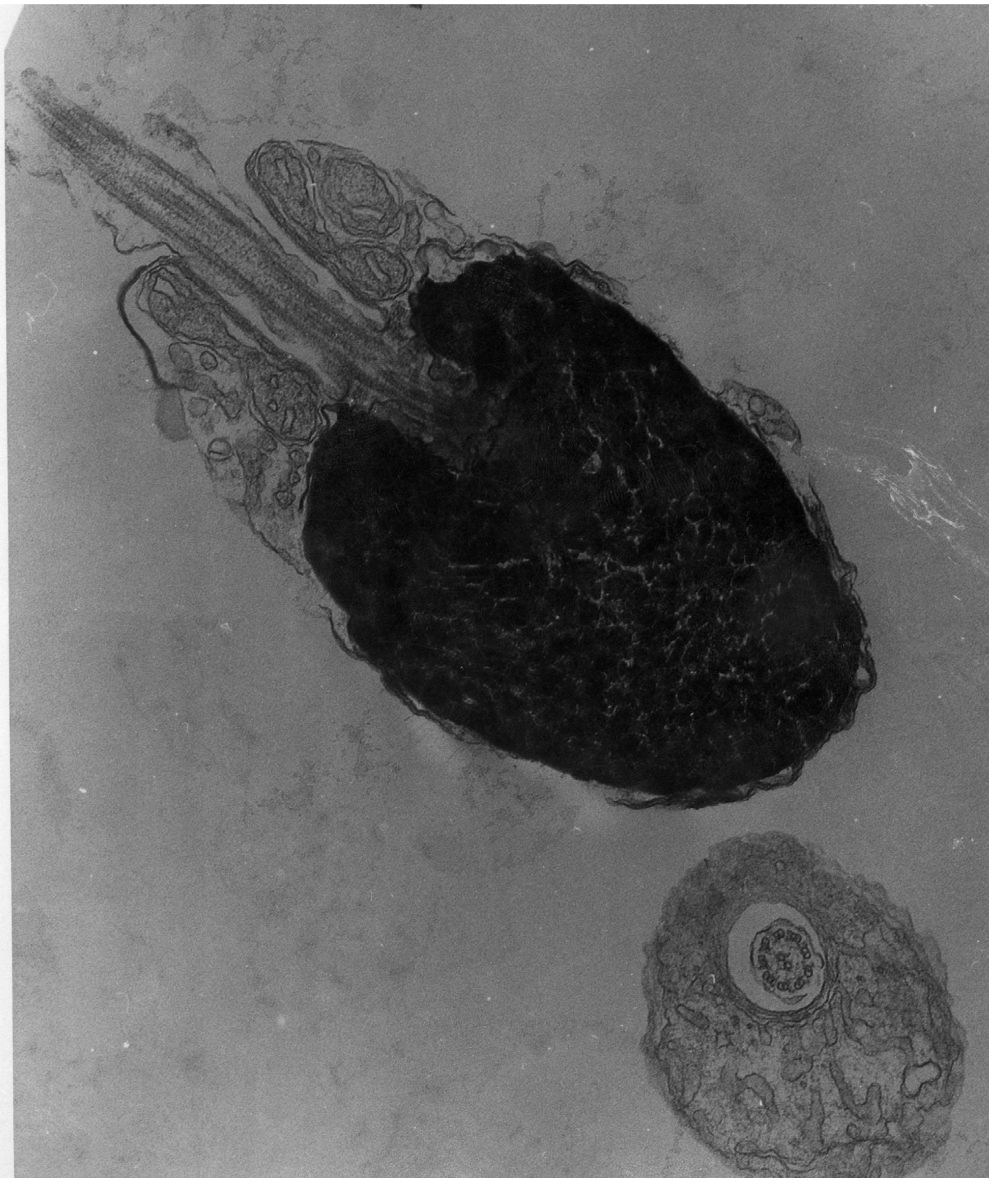

Fig. 1. Electron micrograph showing a longitudinal section through sperm head and middle piece of a salmon. Sperm nucleus contains densely packed chromatine, which is transcriptionally inactive. Below, a transverse section of the middle piece. Note the cell membrane around the sperm head and a single circular mitochondrion in the middle piece. On the transverse section of the middle piece the axoneme with a typical 9+2 microtubular complement is apparent. Magnification x 40 000. Courtesy by Björn Afzelius (reprinted from Vladić 2001, with permission).

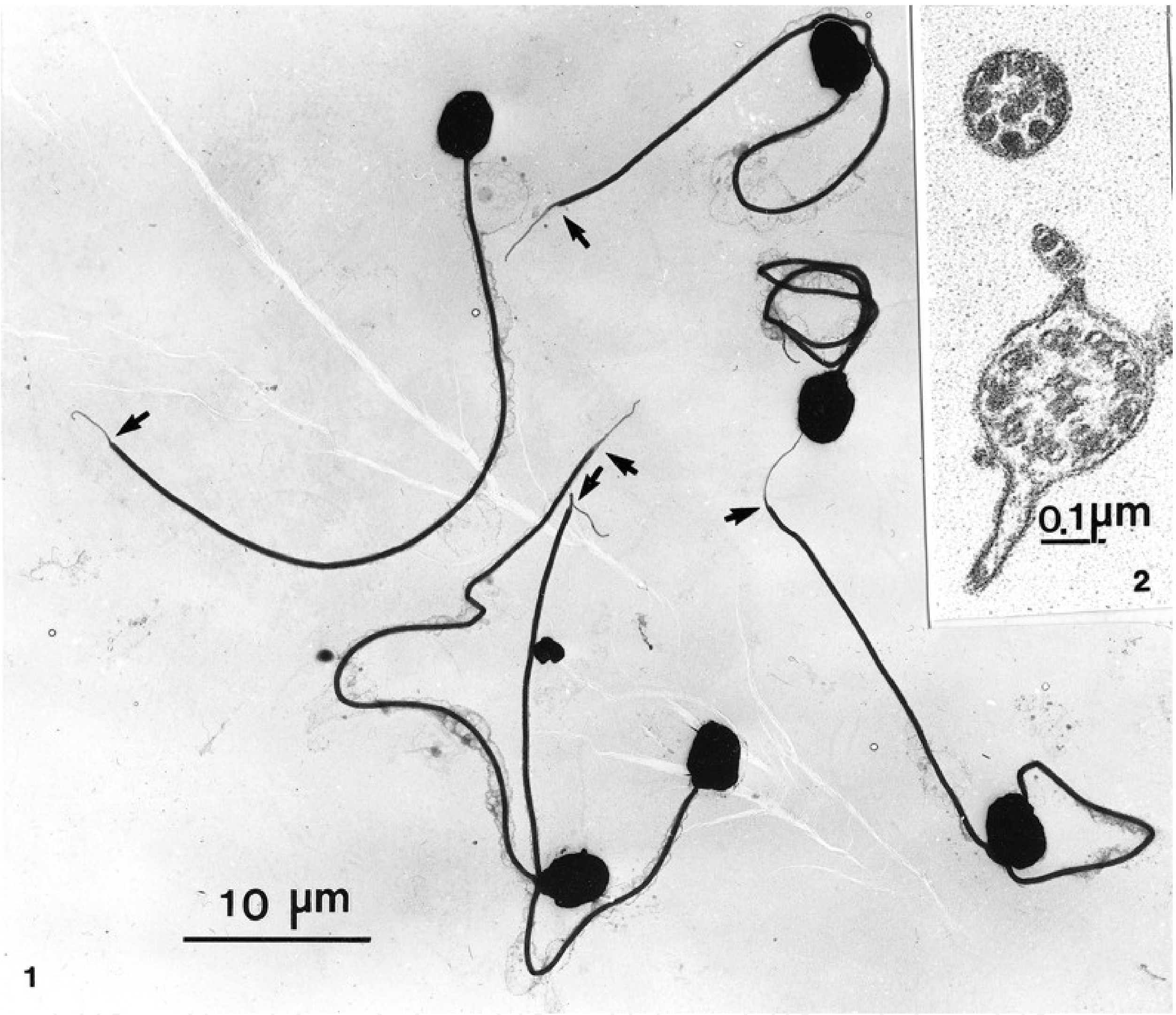

Fig. 2. 1) Whole mount of spermatozoa from a salmon parr. X2200. At the end of flagella, tail tip, containing only two centrally positioned, inner microtubules are indicated (arrows). 2) Sections through sperm tails from an anadromous salmon. The transected main piece (bottom) has nine microtubular doublets carrying inner and outer dynein arms and the two inner microtubules; the cell membrane forms two side fins. The end piece near the upper side fin contains only the two inner microtubules. The upper sperm transect contains 8 + 2 singlets; it is probably close to the transition region. X80 000. (from Vladić, Afzelius & Bronnikov, Biology of Reproduction, 66: 98-105).

4. Sperm may be used either randomly for fertilization depending on their densities in ejaculates (i.e. fair raffle), or spermatozoa originating from competing ejaculates may differ in some features determining mating order or ejaculate quality, leading to different propensities for a success (i.e. loaded raffle). In the *fair* raffle, all sperm compete on equal terms, that is competing ejaculates are physiologically and energetically equal. Thus, only an increased number of spermatozoa relative to competitor's spermatozoa in the competition will yield a greater chance for success in the fair raffle situation. When the physiological quality of spermatozoa differs between competing males, it is expected that sperm quality will determine the outcome of competition. In the *loaded* raffle, a compensatory mechanism is predicted by which males, the sperm of which are devalued, compensate for this disadvantage by expending a greater proportion of reproductive effort on sperm (Parker 1990a,b).
5. In externally fertilizing fish, a female does not exert a direct preference for the competing ejaculates.

If males have an imperfect information about the role in sperm competition (eg. mating hierarchy), sperm expenditure should increase proportionally with the risk of sperm competition (Parker 1990a). The mating role (dominant or sub-ordinate) doesn´t have to be randomly assigned, like in the mating systems in which male characters correlated with fitness, like body size, determine dominance and access to females. Males in disfavoured role are here expected to compensate for mating disadvantage by expending a greater proportion of reproductive effort on sperm production than males in dominant role. Dominant males are likely to suffer an informational handicap making them uncertain of engagement in sperm competition. This informational handicap of dominant males favours sneaking tactic, which attains significantly greater paternity than dominant adult tactic when the probability of cuckolding (mating out of pair bond) is low, but not when the intensity of sperm competition is high (Parker 1990b). The reason for the latter expectation is that an increase in the number of players (ejaculates) in competition results in reduced pay-offs when the number of players is greater than 2 (Parker 1998). Therefore, disfavoured males ought to be selected to expand more energy in sperm production and/or quality than dominant males (Parker 1998).

In all salmonid species, there are at least two distinct life histories in males (Jones, 1959; Fleming 1996): one, with dominant anadromous males with variable degrees of fighting ability that have developed linear dominance hierarchy, and second, with small precociously mature males- parr that do not migrate to sea to acquire food for prolonged growth, but stay in the stream of their hatching or ″grilse″, who return to the spawning ground after single season in the sea. Because of the smaller amounts of food in the river, and different ecological conditions of the freshwater habitat (reviewed by Gibson, 1993) these males are miniature in size relative to dominant males (Gage et al 1995) (Figure 3). In salmonids, genes are propagated into future generations by means of alternative life history strategies. Thus, younger, precociously mature males are using ″sneaking″ tactic in the vicinity of the spawning salmon pair - after it have swam unnoticed into the spawning territory where dominant male have already courted a female, parr is trying to ″sneak″ into the sperm cloud of dominant male ejaculates, when it will also ejaculate spermatozoa in what is to be a trial to fertilize females eggs in the red (Figures 4 and 5). This strategy can be very costly for pre-cocious parr if discovered by dominant male, because dominant will not hesitate to retaliate. Such retaliatory behaviour can sometimes incure injuries, or even death of precocious salmon parr (Hutchings & Myers, 1987). Reproductive strategies can be defined as genetically based behavioural programmes influencing individual allocation decisions to reproductive effort between alternative tactics within a sex (Gross 1996). Phenotypes that became as coevolved responses of life history traits to ecological problems are alternative life history tactics (Stearns 1976). The alternative strategy involves a genetically based life history program, which has evolved under environmental, usually frequency-dependent selective pressure (Gross 1996). When average individuals have reduced fitness compared to individuals on extremes of phenotypic distribution, disruptive selection might select for extreme individuals (Rueffler et al 2006). Variability in response to environmental pressure among individuals within salmonid populations is shaped by differences in survival and reproductive success.

Atlantic salmon (Salmo salar) is an anadromous species, which spawn in freshwater, a feature characteristic for all salmonids. During its life history, two ecological environments are inhabited, a freshwater environment, in which salmon hatch and spawn, and a marine environment, where fast growth is achieved. The seaward migration is preceded by one to eight years. Before returning to the river of hatching for spawning the anadromous males and females stay between one and five years in the sea. Immature fish in the river (parr), become smolt in the spring of the second, third or fourth year. The process of smoltification involves various morphological, behavioural and physiological changes, as adaptations to marine environment. Salmon that return to the spawning river after only a single year are called 'grilse' (Mills 1971). Salmon do not feed during spawning migration, when males develop conspicuous lower hook and red bodily coloration, viz. secondary sexual characters (Figure 3). In northern latitudes, spawning may last from October to February, depending on duration of returning time to the nascent river. Males contribute no nest guarding or offspring tending to the female, but only their spermatozoa. Although after the spawning most of the males (called 'kelts') die due to high energetic costs that are paid in terms of intra-sexual fights for female acquisition and metabolic demands of sexual maturation (Jonsson et al 1991), relatively small proportion of females return to spawn in the following season (Mills 1971). Sea trout (*Salmo trutta*) males pursue shorter migratory routes and have greater iteroparity (i.e. mating in several consecutive seasons) than Atlatic salmon males, which undertake long migrations to the feeding grounds far off the coast and have an increased mortality rate after single spawning season (i.e. semelparity) (Belding 1934, Jones 1959, Mills 1989). Alternative male sexual maturation strategies are apparent both in salmon and brown trout, with adult, anadromous males which shed sperm simultaneously with precociously mature parr, a situation which results in sperm competition (Fig. 3). Number of males that may compete over fertilization of a single female eggs can vary between one and ten males (Hutchings 1986, Petersson and Järvi 1997). Gonad maturation was proposed to be determined by a genetical threshold (Thorpe 1986), which in concert with environmental control of maturation (shortening photoperiods; Lundqvist 1980; higher-than-average temperatures; Adams and Thorpe 1989; and food in excess enabling good growth, Alm 1959) determines male maturation pattern. Males that have a good growth rate tend to mature precociously (Alm 1959); they are maturing as precocious parr (Jones 1959, Mills 1989). A genetic component in male reproductive strategies was found in the Atlantic salmon (Glebe and Saunders 1986; Garant et al 2003). Individual precociously mature Atlantic salmon parr males have very variable fertilization success and may fertilize up to 65% of female eggs in the redd (Hutchings and Myers 1988, Thomaz et al 1997; Garcia-Vazquez et al 2002).

Precocious parr invest relatively more into gonadal tissue for their body mass than anadromous adults which invest more into secondary sexual traits which are frequently used in aggressive intrasexual interactions (Vladić & Järvi 2001). Also, higher metabolic demands of the parr reproductive strategy may be the reason that the relative heart weight in precocious parr is greater than this in immature fish (Armstrong and West 1994). This life history strategy is also associated with the impaired sea-water adaptability and reduced smoltification (Myers 1984, Lundqvist et al 1989). Male success is more dependent on social environment than is female success, which is dependent on the allometric relation between body size and gonad mass; therefore no single optimal life history is expected (Thorpe et al. 1998). Several decisions about the number of winters in the sea before returning to spawning may be exhibited within a single cohort. This results in the variable proportions of precociously mature parr, "grilse" and anadromous males that have spent a varying number of years in sea (Thorpe et al. 1998).

In reproductive biology, male quality equals individual reproductive success. Sperm movement in externally fertlizing fish is dependent on the cellular energy, produced in the mitochondria located in the sperm mid-piece. The synthesis of ATP is coupled to respiratory electron transport requiring the expression of mitochondrial genes. As the sperm cytoskeletal microtubular assembly, the axoneme, is extending throughout the sperm flagellum, sperm size is mainly related to sperm tail length (reviews in Gibbons 1981, Witman 1990). Reduction in sperm size with the increase in time between ejaculation and fertilization of the egg was predicted when the sperm tail size is positively correlated with sperm velocity at the expense of sperm longevity (Parker 1993). This prediction is applicable typically to internally fertilizing species**.** The logic is that it is difficult to adjust sperm size before given mating, since sperm have matured in the reproductive tract before the information about the role in competition could influence male ejaculation tactic. In externally fertilizing species, like salmon, it was found that sperm size decreases with sperm competition across fish species (Stockley et al 1997). In the Atlantic salmon, positive associations between different sperm length parameters and sperm energy charge, ATP concentrations and fertilization ability were found (Vladić et al 2002). In addition, salmonid sperm show adaptation to natural spawning temperatures (ie 3-4 ºC), whereas trout eggs exhibit higher thermotolerance than salmon eggs, possibly reflecting the southern origin of trout (Vladić & Järvi 1997). Sperm density was higher in both brown trout and salmon precocious parr, whereas salmon sperm are containing greater ATP concentrations than trout sperm (Vladić 2001). These features may be connected to the greater semelparity of salmon as compared to trout (Vladić 2000). Jonsson and Jonsson (2005) discuss greater energy allocation in reproduction of the precocially mature parr of Atlantic salmon than this in precocially mature trout parr in connection to conspicuous body size difference between the species and relatively longer migration distances to the feeding areas at sea in the Atlantic salmon as compared to the brown trout. Female eggs were found to be fertile after 512 s in water, significantly longer than sperm were mobile, i.e. 100-300 s at 2-4 Cº (Vladić & Järvi 1997). Salmon parr have greater sperm vigour (percentage of motile cells in ejaculates) (Vladić & Järvi 2001) and trade-off between sperm velocity and longevity after one-third of time since sperm activation (Vladić 2001), the result in agreement with the result published by Levitan (2000) (see Rosengrave et al 2009 for the discussion of effect of ovarian fluid on sperm behaviour). Therefore, studies on sperm traits should not imply contention of individual male quality unless these traits are tested in fertilization experiments. Besides sperm ATP content, sperm velocity was found to be the most important determinant of success in sperm competition (Gage et al 2004; Burness et al 2004; Yeates et al 2007). In addition, salmon parr were found to produce more ATP per sperm cell and are beter in fertilizing eggs both in the non-competitive situation (Vladić & Järvi 2001) and in sperm competition (Vladić et al 2010) confirming thereby the loaded model of sperm competition (Parker 1998).

Sperm density in the competition is high; therefore all eggs in externally fertilizing fish are expected to be fertilized instantaneously. At ESS, there will be a natural level of egg loss due to sperm death rate (Ball and Parker 1996). This "adaptive infertility" is opposed by an increase in sperm competition intensity; it benefits females to tolerate group spawning promoting thereby conflict between males and thereby sperm competition (Ball and Parker 1997). In addition, trade-off between offspring quality and quantity might be expected. This emanates from the fact that in structured populations, natural selection does not maximise short-term individual reproductive success (quality) but rather long-term value associated with genotype distribution in the population (McNamara et al 2011).

4. Human impact on salmonid ejaculate allocation and heritability of phenotypic plasticity

Human impact on wild habitats has proven devastating in many instances, as a consequence of the extensive hydroelectric power plants dam construction in most Swedish rivers. Occurrence of interspecific hybrids between the salmon and trout, which are called "laxing" in Sweden, was attributed to the shrinkage of the spawning area and destruction of natural spawning habitats caused by new hydroelectric plants (Jansson and Öst 1997). Such inter-specific hybrids are sterile. In addition, wild-farmed Atlantic salmon hybrids were found to have lowered fitness in comparison to wild fish, cautioning that frequent escapes from hatchery facilities may potentially reduce fitness for wild populations (Fleming et al 2000; McGinnity et al 2003; Araki et al 2007). Therefore, hatchery rearing for compensatory purposes has created new demographic pressures on endangered wild populations of these fish. Some traits are artificially selected for in hatchery environment, like genes for pathogen resistance (reviewed by Fjaelstad et al 1993), for instance genes of the Major Histocomapatibility Complex (MHC) that confer resistence to disease in vertebrates (Reusch et al 2001). However, considering the fact that local populations contain long-term adapted genomes to local environments, gene flow between farmed and wild fishes is likely to erode local adaptation and possibly lead to their extinction (McGinnity et al 2003). Hereditary basis for age at maturity in salmonids cautions that the compensatory breeding programs could have a significant demographic influence on wild Atlantic salmon populations (see Garant et al 2003), since the proportion of early maturing males may be substantial in hatcheries from where the supplementary fish are recruited, especially under favourable conditions of culture (i.e. higher-than-average temperature, food in excess) (reviewed by Jonsson & Jonsson 2006). Therefore a knowledge about ejaculate quality from alternative male morphotypes commonly engaging in sperm competition at spawning grounds has comprehensive areas of application, from those related to basic evolutionary questions to application of the findings in species management context.

Fig. 3. Differences in size between andromous and preciously mature parr of sea trout (above) and salmon from river Dalälven (below), showing the asymmetry in roles that these male morphotypes experience during sperm competition. Below, at the top, a female (81 cm long, 5.2 kg total weight), beneath a male (92 cm long, 6.7 kg total weight) with a large kype at the lower jaw, elongated nose and big adipose fin. The three smaller salmon are mature parr. Note differences in body morphology between parr males and anadromous adults, and differences in the expression of secondary sexual traits between the anadromous male, the female and precocious parr. Photo by Erik Petersson and Anna Löf. (Lower photo reprinted by permission from Vladić 2001, with permission).

Fig. 4. Sea trout precocious parr assumes an advantageous ″sneaking″ position beneath the female genital vent. Photo: Tomislav Vladić.

Fig. 5. Orgasm and ejaculation of an anadromous trout male. The female that expulsed eggs is behind the ejaculating male. Note the precocious parr in the sperm cloud beneath the anadromous male; it released sperm in sperm competition. Photo: Tomislav Vladić.

Since behaviourally sub-ordinate males can acquire fitness benefits by exploiting sexual investment of behaviourally dominant males, male-biased operational sex ratio selects for alternative reproductive tactics, possibly through frequency-dependent selection. Conditional variation (variation depending on environmental influence) may produce different phenotypes from single genotype (Gross 1996). Reaction norms are genotype responses describing the manner individuals respond to environmental change within a population (Woltereck 1909). In salmonid fishes, growth rates influence choice of male mating tactic; males in good condition tend to mature early whereas males in poor condition tend to postpone reproduction in favour of prolonged body growth (Hutchings & Myers 1994; Thorpe et al 1998). This choice is a "threshold trait", where a liability toward maturation-age decision depends on the phenotype's position relative to some physiological (or environmental, see below) threshold value. It is evident that human impact exercised through high food ratios supplemented to hatchery fish aimed at compensatory releases changes male maturation pattern in the population, since conditional variation produces different phenotypes from the same genotype over environmental gradient (i.e. phenotypic plasticity). Therefore, decrease in egg size is expected when the food supplementation is in excess in hatcheries (Heath et al 2003), as offspring from larger eggs could have an advantage early in life (Einum & Fleming 1999). Interestingly, brown trout sea-running males were found to preferentially fertilize eggs of intermediate sizes, on the contrary to precocially maturing parr, which fertilized all eggs sizes indiscriminately; this mechanism was proposed as an expression of cryptic male choice (Vladić 2006). Recently, phenotypic plasticity in sperm production as a response to sperm competition risk was emphasized (Rudolfsen et al 2006; Cornwallis & Birkhead 2007; Pizzari et al 2007; Ota et al 2010).

Importantly for conditional strategies to evolve, environmental cue affecting gonad maturation must be reliable, whereas finesses of the alternative maturation life histories are not necessarily equal (Tomkins & Hazel 2008). Each reaction norm can be understood as different conditional strategy. A cue property of the genetic response in reaction norms as a result of selection, G, is that the selection differential before and after the episode of selection measured by mean mortality in different environments, S_k, and heritability of the plastic maturation trait, h^2, will vary in the function of environmental cue distribution, e, (e.g. feeding, temperature, photoperiod) within a given generation k:

$$\Delta G_k = \frac{S_k h^2}{e} \tag{2}$$

Evolutionary changes arise through change in frequency distribution of the environmental cue, each side of this distribution favoring different maturation conditional tactic (eg. early versus late maturing phenotypes) (Tomkins & Hazel 2008). Above equation implies that stronger additive genetic variation for the maturation trait, the stronger response to selection should be over an environmental gradient.

Heritability of phenotypic plasticity depends on the extent of genotype *x* environment interaction and strength of sexual selection. A genotype *x* environment reaction exists in the population if slopes of alternative fitness functions over environmental gradient cross. If slopes of fitness functions do not cross, male tactic may depend on individual male condition, which is commonly influenced by developmental constraints (Tomkins & Hazel 2008). These conditional reproductive tactics are central in sexual selection. Thus, genetic variance in phenotypic plasticity in the population, δ^2_{PL}, can be defined by partitioning total variance,

$$\delta^2_{PL} = \delta^2_E + \delta^2_{GxE} + \delta^2_S \tag{3}$$

where δ^2_E is environmental variance, δ^2_{GxE} is genotype *x* environment variance and δ^2_S is conditional variance due to sexual selection. Reduced phenotypic plasticity due to interbreeding between escaped farmed and wild fish may reduce capacity of population to cope with environmental change and thereby disrupt population dynamics.

Genetic diversity is crucial in small, isolated wild populations with increased levels of genetic drift, whereby chance events may cause random fixation of deleterious or invasive alleles. Maintaining genetic diversity and minimizing potential bottlenecks due to genetic drift requires minimum relatedness among individuals (Ohta 1982). In the generation *k*, genetic diversity can be defined as

$$\mathrm{GD}k = 1 - \frac{1}{2Nef} \tag{4}$$

where $2N_{ef}$ is the effective allele number (Crow & Kimura 1970; Caballero & Toro 2000). Common procedure employed in hatcheries is to mix ova from several females with sperm from several males in a single batch for supportive breeding purposes. This procedure induces sperm competition leading to reduction in the effective sample size of breeders and to increase in genetic variance in the population (Withler 1988; Withler & Beacham 1994). Although sperm potency leads to increased individual fertilization success, it may also lead to decreased genetic variation within populations when sperm traits are heritable due to increased variance in fertilization success between competing males and consequently decreased effective population size. Therefore equalizing milt volume in hatcheries should not necessarily reduce loss of genetic variation even at expense of favouring younger males in competition (Vladić et al 2010), because this practice reduces opportunity for natural selection to cleanse locally maladapted genetic contribution (Wedenkind et al 2007).

Effective number of breeders is defined as (Ridley 1993):

$$Ne = \frac{4NmNf}{Nm + Nf} \tag{5}$$

where *Ne* is the effective number of breeders contributing to the gene pool in the following generation, Nm and Nf are numbers of male and female breeders, respectively. N*e* is the effective size of population with Mendelian segregation of genes (ideal population: equal sex ratio, constant population size and random probability of survival to adulthood) derived from the probability that two alleles at a locus are derived from the same grandparent. Means and variances are derived from the numbers of offspring surviving to maturity rather than from individual reproductive success (Campton 2004). Numbers of offspring surviving to maturity are affected by life history patterns of fish under consideration, as it was shown that salmon precocious parr males produce ejaculates of greater quality (Vladić & Järvi 2001: Vladić et al 2010), in accordance with predicted inverse relationship between fish age and gamete quality (Fleming 1996). Therefore, maximizing number of founders is expected to maximize genetic diversity in the population.

To summarize, genetic effects of captive breeding in hatcheries for supplementation of wild fish after destruction of natural spawning paths due to building of artificial dams for power-plant energy production may create fish that are reproductively inferior in the wild (Fleming et al 2000; Araki et al 2007). Nevertheless, negative effects of fish supplementation might be dependent on species and on the fish strain, since detrimental effects of the seven generation rearing on reproductive performance were not found in the brown trout from the river Dalälven stock (Dannewitz et al 2004).

5. Sperm competition and maternal effects

Rather than paternal, maternal genes were found to influence sperm phenotype (Froman & Kirby 2005), including sperm length in *Callosobrushus maculates* (Gay et al 2009). In addition to effects on sperm size, maternal genes strongly influence sperm motility, notably through predominantly (see Ankel-Simons & Cummins 1996; Rand 2001) maternally inherited haploid mtDNA (Ruiz-Pesini et al 2000; Froman & Kirby 2005). Selective forces are expected to differ between internally and externally fertilizing species due to discrete differences in the physical environment in which sperm compete to fertilize eggs. In externally fertilizing species where fertilization occurs instantaneously and sperm are relatively short-lived, sperm velocity may be naturally selected trait that confers advantage in competition for fertilizations. Nevertheless, in cases when insemination and fertilization are temporally separated as is the case for most internally fertilizing species, different sperm traits might be selected for (Parker 1993). In such cases, sperm longevity should be selected for (Taborsky 1998). Therefore, we expect that selective forces shape different ejaculate traits, which are advantageous depending of the mode of reproduction. In addition, sperm quality and quantity may trade off due to constraints imposed by conflicting life-history demands of simultaneous investment in body growth and gamete quality (Stearns 1992). However, if sperm quality and morphology are polygenic and/or unlinked traits, we should not expect to detect simple correlation between gamete quality and morphology.

Sexual selection selects for the two male traits: intrinsic genetic quality (indirect mechanism) and paternal care (direct mechanism). There is no paternal care in salmonid fishes. Body size is the male trait directly preferred by females (Andersson & Simmons 2006); the mechanism suggested by which a cryptic female choice for male's genetic quality is exerted in externally fertilising fish is through ovarian fluid that facilitates sperm function in the Arctic charr (Turner and Montgomerie 2002) and in the Atlantic cod (Litvak and Trippel 1998). The effect of ovarian fluid on sperm performance depends on the physiological compatibility between male and female partners (Rosengrave et al 2008). Mate choice is believed to optimize variation on Major Histocompatibility Complex (MHC) genes that confer resistance to disease. However, in the brown trout, female eggs were fertilized preferentially by males with intermediate molecular divergence in MHC genes, as males with great amino acid divergence on the MHC loci might have lower adaptation to locally adapted pathogens (Forsberg et al 2007). In the Atlantic salmon, variation in the MHC I class gene was biased toward similar genotypes, suggesting thus suppression of hybridization and outbreeding depression as the possible mechanism in salmonid mate choice (Yeates et al 2009). Thus, local adaptation may be disrupted by interbreeding between wild and escaped farmed fish in small isolated wild populations (reviewed by Hutchings and Fraser 2006).

6. Conclusions and future perspectives

Salmonid reproductive strategies are determined by intrasexual competition between males for fertilization and by female body condition. Human interruption in natural spawning that is practiced in hatcheries during compensatory breeding programmes can potentially diminish stock genetic diversity. Therefore it is a task of utmost importance to understand processes that intervene with the evolutionary mechanisms that maintain alternative reproductive phenotypes in the remaining natural salmonid populations. Some questions are unanswered still:

1. How to maintain current levels of aquacultural production without simultaneously reducing existing wild fish stocks genetic diversity due to interbreeding of escaped with wild fish?
2. Perform hatchery precociously mature parr males “the best of a bad job” strategy or produce ejaculates of greater quality than their wild counterparts?
3. What costs, if any, do wild females pay if mated with precociously mature parr males originating from hatcheries?

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