Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*

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Abstract

Long-term data from underwater video recordings in the wild and semi-natural channels are compared to the current literature to review the reproductive behaviour of fishes in the subfamily Salmoninae. Male alternative strategies and tactics are discussed. Reproductive behaviour in Salmoninae is divided into different phases related to female nest selection, construction, and completion. Still underwater video frames are used to support conclusions drawn on spawning behaviour.

Introduction

Salmoninae nest building behaviour provides ideal opportunities for behavioural studies. Pioneering works by Jones and King (1949, 1950, 1952) with Atlantic salmon (*Salmo salar*); Jones and Ball (1954) with brown trout (*Salmo trutta*) and Atlantic salmon; Fabricius (1953) and Fabricius and

Gustafson (1954) with arctic charr (*Salvelinus alpinus*) described detailed breeding patterns for these species. These works were based on extensive observations in aquaria and semi-natural channels. In some studies, live observations were supported with underwater film recordings used for further analyses. As a result, hypothetical adaptive values for various behavioural patterns observed during spawning were described. More recently, many other authors have investigated Salmoninae spawning behaviours in detail (Chebanov, 1980 (pink salmon; *Oncorhynchus gorbuscha*); Newcombe and Hartman, 1980 (rainbow trout; *Oncorhynchus mykiss*); Leggett, 1980 (dolly varden; *Salvelinus malma*); Schroder, 1981 and 1982 (chum salmon; *Oncorhynchus keta*); Foote, 1987 (sockeye salmon; *Oncorhynchus nerka*); Sigurjónsdóttir and Gunnarsson, 1989 (arctic charr; *Salvelinus alpinus*); Evans, 1994 (sea trout; *Salmo trutta*); Fleming, 1996 (Atlantic salmon); James and Sexauer, 1997 (bull trout; *Salvelinus confluentus*); Healey and Prince, 1998 (coho salmon; *Oncorhynchus kisutch*); Blanchfield and Ridgway, 1999 (brook trout; *Salvelinus fontinalis*); Berejikian et al., 2000 (chinook salmon; *Oncorhynchus tshawytscha*); for a more detailed review see Fleming, 1998). Other scientists have discussed different aspects of the salmonines breeding ecology (Beacham and Murray, 1985) for morphological differences in spawning Pacific salmon across latitude; Foote (1988) for male choice in kokanee and sockeye salmon; Crisp and Carling (1989) for redd morphology; Foote (1990) for the role of territoriality during spawning in sockeye salmon; Jonsson et al. (1991) for the energetic cost of spawning in Atlantic salmon; Barlaup et al. (1994) for female behavioural variations in the genus *Salmo*; Quinn (1999) for differences within three *Oncorhynchus* species spawning in sympatry).

As native wild salmonid populations have declined and hatcheries and farming activities have increased, concern about the genetic integrity of salmon populations has grown. As a result, research has been directed towards possible behavioural differences in mating that may reproductively isolate wild populations from escaped hatchery or farmed fish (Fleming and Gross, 1993; Fleming et al., 1996; Berejikian et al., 1997; Petersson and Järvi, 1997; Chebanov and Riddell, 1998; Fleming and Petersson, 2001). Despite the large amount of early work done on salmonines, a detailed and rigorous description of spawning behaviours in the wild is still needed. This manuscript uses long term observations and underwater video recordings in the wild and in semi-natural channels together with literature references to review how *Oncorhynchus*, *Salmo*, and *Salvelinus* behave during reproduction. Other Salmoninae genera such as *Brachymystax*, *Hucho*, and *Salmothymus* are poorly known and their reproductive biology remains a fascinating line of future research.

Overview of the Salmoninae mating system

Mating systems reflect the number of mates an individual acquires per breeding attempt, conflicts between the two sexes and how they are resolved (Berglund, 1997). Anisogamy, or the condition where females and males produce gametes of different sizes (Bateman, 1948), and 'differential parental investment' or the differential allocation of energy in offspring production and subsequent care females and males provide (Trivers, 1972) have shaped the role of each sex during reproduction. Males maximize their reproductive success quantitatively, by mating with as many females as possible, whereas females qualitatively, by choosing appropriate nest sites and quality males (Gaudemar, 1998; Quinn, 2005).

Salmoninae males compete for access to females, which are, as in most other vertebrate species, thought to be the limiting resource (Darwin, 1871; Gross, 1984; Anderson, 1994; Fleming, 1996; Blanchfield and Ridgway, 1999; Garant et al., 2001). Females compete for space to establish their nests (Fleming and Gross, 1994; Fleming, 1998). They select nesting areas (redds) and dig a series of depressions (nests) to successively deposit their eggs (Groot, 1996; Gaudemar, 1998). The strong male–male competition characteristic of Salmoninae often results in a few males mating with several females (Schroder, 1981). Females can also spawn with many males in a single spawning act or with different males in successive acts (Garant et al., 2001). Salmonid spawning results in a multiple polygamous system in which the five forms of mate competition are present: termed contests, mate choice, endurance rivalry, scramble competition, and sperm competition (Andersson, 1994).

Termed contests refer to fighting displays or actual fights over mates. Male–male competition is probably the most studied aspect of the Salmoninae mating system. Salmoninae males fight ferociously for spawning access (Keenleyside and Dupuis, 1988b). Normally size and morphology determine the outcome of such fights, larger males with well developed secondary sexual characters having an advantage over smaller rivals (Schroder, 1981; Keenleyside and Dupuis, 1988b; Järvi, 1990; Fleming and Gross, 1993; Kitano, 1996; James and Sexauer, 1997; Foote et al., 1997). However, even large males fail to monopolize spawnings due to competition. This concept has led to discussions of hypothetical alternative male reproductive strategies and tactics (Gross, 1984, 1985, 1996; Taborsky, 1994; Healey and Prince, 1998).

Mate choice refers to behavioural and morphological traits that attract and stimulate mates (Andersson, 1994). Female choice in salmonines has been suggested to be overruled by male–male competition (Fleming and Gross, 1994; Quinn and Foote, 1994; Petersson et al., 1999). This idea, based on the supremacy of large dominating males in the spawning grounds, only allowed females a passive role in spawning activity. Nevertheless, females have been reported to exhibit their choice by frequently attacking smaller males (Berst et al., 1981; Keenleyside and Dupuis, 1988b; Järvi, 1990; Petersson and Järvi, 1997; Berejikian et al., 1997), and by delaying spawning when courted by non-desirable males (Schroder, 1981; Foote, 1988, 1989; Foote and Larkin, 1988; Blanchfield and Ridgway, 1999; Berejikian et al., 2000; Gaudemar et al., 2000b). Delaying spawning is a form of choice by which females increase their chances of being joined by larger or more fit males. However, the opposite, accelerating spawning when being courted by a desirable male, has not yet been discussed (but see Schroder, 1981).

Endurance rivalry is the ability to remain reproductively active during a large part of the breeding season (Andersson, 1994). Males' longer life at the spawning grounds (Fleming et al., 1996; Petersson and Järvi, 1997; Hamon et al., 1999) and protandry, or the earlier arrival of males to the spawning grounds than females (Johnson, 1980; Morbey, 2000) are two known characteristics that differentiate males and females during spawning. However, no studies have determined whether differential reproductive success is associated with endurance rivalry in males. According to Andersson (1994) larger body sizes should favour longer life spans, because maximum storage capacity increases with body size more rapidly than metabolic costs. If this is the case, the greater reproductive success of larger males may not only be a consequence of their fighting abilities, but also from greater endurance resulting from their large size.

Scramble competition describes the ability to find mates when a large number of females become available simultaneously or a large number of males must compete for them in a limited area (Alcock, 1993). In a system where dominating males guard females and prevent other males from approaching, the ability to obtain fertilizations by "sneaking" plays a definitive role. This has even more importance as the spawning season progresses and (due to differences in duration of sexual activity in males and females) the ratio between sexually active males and females increases (Quinn et al., 1996; Gaudemar, 1998; Quinn, 2005).

Sperm competition can be defined as competition between the sperm of two or more males in their efforts to fertilize the eggs of a single female (Taborsky, 1998). Even though, a hierarchy of males around a nesting female will generally be well established some time before gametes are released, in the end, sperm competition inevitably takes place (Hoysak and Liley, 2001). This occurs when several satellite males simultaneously emit sperm. Paternity analyses have shown that males closest to the female at the time of the spawning fertilize most of the eggs (Mjølnerød et al., 1998). However, distance from the female and timing of sperm release are not the only factors. Sperm volume, velocity and viability, are also important (Hoysak et al., 2004). Additionally, smaller males, forced by larger competitors to maintain a distance from the female, can overcome this handicap by positioning their vent closer to the female's during spawning (Foote et al., 1997).

Alternative male reproductive strategies and tactics

Depending upon their age at maturation, salmonine males can adopt three strategies: mature as older, younger, or precocious males (Fleming, 1996,

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1998). This in turn is associated with size, with the largest individuals normally being the ones staying longest in feeding area (but see Quinn and Foote, 1994). In addition, salmonines, depending upon their behaviour at the spawning grounds, can employ two tactics to achieve fertilizations; either they fight or they sneak (Gross, 1984).

Strategies are irreversible and conditioned to certain physiological thresholds thought to have a genetic–environmental basis (Bohlin, 1990; Hutchings and Myers, 1994; Silverstein et al., 1997; Fleming, 1998; Healey and Prince, 1998), being age at maturity inversely related to growth rate (Metcalfe et al., 1989; Thorpe, 1989, 1994; Henson and Warner, 1997; Unwin et al., 1999). However, males surviving spawning (iteroparous species) can adopt different strategies through their lifetime. A precocious male, for instance, can smolt some months after spawning and complete its ocean phase returning to the spawning grounds as a younger or as an older male (Wilson, 1997). In contrast, tactics are reversible; males can switch back and forth between them depending on the types of rivals encountered (Foote and Larkin, 1988). The relative size between male rivals is the best predictor for the spawning tactics that will be employed (Chebanov, 1980; Foote, 1990; Healey and Prince, 1998; Yamamoto and Edo, 2002). However, relative size is not the only factor contributing to the tactics employed, frequently newly arrived young males will fight and successfully defeat larger males debilitated as the spawning season progresses (personal observations). In addition, a male can simultaneously use two tactics with different rivals; he can, for instance act as a fighter when faced with a similar-sized male and as a sneaker when confronted with a larger one.

The older male's strategy

Some males stay in the feeding area (ocean, lake, or river) for a longer period of time than others. Different terminology depending on the particular species life histories or morphology has been used to name these fish (e.g. multi-sea winter males, hooknose males; for additional nomenclature see Quinn, 2005). Normally, the tactic employed by large males is to fight other rivals and establish dominance around nesting females (Healey and Prince, 1998; Figures 1 and 2). Males losing these battles can either adopt a subdominant or "satellite" position downstream from the focal female, or search for other available females (personal observations). Alternatively, males can directly adopt the tactic of a satellite fish.

The younger male's strategy

A male can mature after a shorter period of growth and return to the spawning grounds at an intermediate size. Different terminology depending on the particular species life histories or morphology has been used to name these fish (e.g. grilse males for Atlantic salmon and jack males for the Pacific salmons; Quinn, 2005). These fish have several options: they can search for females not defended by large males and fight other young males for dominance. Alternatively they can join large males and fight with subdominant fish to maintain a lead position among the satellites. However, young males in the presence of bigger fish will normally adopt a sneaking tactic (Healey and Prince, 1998). Sneakers wait for the moment of spawning from a strategic position away from fighting males. At the moment of egg release they take advantage of their smaller size to take a position closer the female's vent (Hanson and Smith, 1967; Gross, 1984; Foote et al., 1997). An alternative method for smaller or intermediate size males to achieve fertilizations is to mimic females (Schroder, 1981; Sigurjónsdóttir and Gunnarsson, 1989; Keenleyside and Dupuis, 1988b; Figure 3). By adopting female coloration and behaviours, males can remain close to females without being

Figure 1. Sockeye salmon males fighting for total dominance in the redd.

Figure 2. Chum salmon males fighting for total dominance in the redd.

Figure 3. Chum salmon male resembles a female in coloration and morphology.

attacked by other males, and fertilize adjacent eggs by ''sneaking'' (Groot, 1996).

The precocious male's strategy

A male can mature at the parr stage before moving to alternative feeding habitats (Table 1). The precocious parr behaviour and reproductive success has been extensively studied in Atlantic salmon (Jones and King, 1952; Myers and Hatchings, 1987; García de Leániz, 1990; Garant et al., 2001; García-Vazquez et al., 2001; Taggart et al., 2001). Precocious males wait for spawning events from hidden positions within the redd or in refuges in the near vicinity (Jones and King, 1952; Fleming 1996; Figure 4). When adults are not present, the parr fight each other to have a privileged position in the nest (personal observations). As a result of these contests generally larger parr occupy the best positions within the redd (Maekawa, 1983; Myers and Hatchings, 1987; Thomaz et al., 1997; Koseki and Maekawa, 2000). However, smaller secondary precocious males are also able to release sperm during spawning by darting into the nest from refuges located outside (Figure 5). Interestingly, female precocious maturation at the parr stage has also been reported in some species, although this is considered very rare (Ivankov et al. 1981; Fleming, 1998).

Mate choice in salmonines

Male choice

Male mate choice is common in animals where females differ in fecundity, mainly in relation to body size (Andersson, 1994). In salmonines fecundity is related to female size (Gaudemar, 1998). Furthermore, bigger females produce bigger eggs and dig deeper nests (van den Berghe and Gross, 1984; Crisp and Carling, 1989). However, behavioural stimuli may be equally or more important than size (Schroder, 1981). Several works have demonstrated that males chose to court those females more actively involved in nest activities independently of their size (Schroder, 1981, 1982; Foote, 1988; Beall and Gaudemar, 1999).

In addition, as demonstrated by Foote (1988) male choice is dependent on male size, small males are less discriminating than larger individuals. This idea relies on the fact that large and powerful males can potentially mate with all available females whereas weaker individuals are limited to lesser mates.

Female choice

Differential behavioural response to male traits can be based on morphological and behavioural characters (Gaudemar et al., 2000b). The effect of male size on female choice has been studied in several Salmoninae species. Females courted by relatively small males delay their spawning activities (Foote, 1988, 1989; Foote and Larkin, 1988; Blanchfield and Ridgway, 1999; Berejikian et al., 2000; Gaudemar et al., 2000b). Schroder (1981) further demonstrated differential spawning

Table 1. Presence (yes) or absence (no) of maturation in the Salmoninae species at the parr stage

Species	Parr maturation	References
Brown Trout	Yes	L'Abeé-Lund et al. (1990), Bachman(1991), Evans (1994)
Atlantic Salmon	Yes	Fleming (1996), Garant et al. (2001), Taggart et al. (2001)
Coho salmon	No	No reports in the literature
Chinook salmon	Yes	Taylor (1989), Healey (1991), Foote et al. (1991), Bernier et al. (1993), Unwin et al. (1999)
Sockeye salmon	No	No reports in the literature
Chum salmon	No	No reports in the literature
Pink salmon	No	No reports in the literature
Masu salmon	Yes	Tsiger et al. (1994), Silverstein et al. (1997), Koseki and Maekawa (2000)
Amago salmon	Yes	Ueda et al. (1983)
Steelhead/rainbow trout	Yes	Needham and Taft (1934), Seamons et al. (2004)
Cutthroat trout	Yes	Fleming (1998)
Brook trout	Yes	Greeley (1932), Blanchfield and Ridgway (1999)
Bull trout	Yes	James and Sexauer (1997)
Dolly Varden	Yes	Maekawa (1983), Maekawa and Hino (1986)
Arctic Charr	Yes	Jonsson and Jonsson (2001)
Lake trout	No	No reports in the literature

velocity based on morphological traits in chum salmon. In this species, dominant males present distinctive vertical colour bars on their sides, whereas subdominant ones have a single horizontal stripe. Females courted by males with stripes slow down nest construction, while those courted by males with bars took less time to construct their nests (Schroder, 1981).

The effect of male courtship activities in female choice has not been studied in detail. The difficulty of this task relies on the complexity of studying behaviour after controlling for size and morphology. Nevertheless, females have been observed to select mates according to the "intensity" of their courtship behaviour (Gaudemar et al., 2000b).

Common conditions contributing to spawning behaviour

Natural selection in terms of the production of offspring and sexual selection in terms of mating

Figure 4. Two Atlantic salmon precocious parr wait for the return of the female to the nest. The parr in the foreground is dominant over the one in the back. The adult fish is an anadromous male.

Figure 5. Atlantic salmon precocious parr (pointed by the arrow) darts into the nest to release sperm.

success have shaped the breeding behaviour of salmonids (Fleming and Gross, 1994; Fleming, 1998; Quinn, 1999). These investigations suggest some common general patterns among species (Groot, 1996).

Salmonines spawn in clean, cold, well-oxygenated waters with gravel bottoms free of silt (Groot, 1996). Some species, or sub-populations of species, spawn in still waters in gravel or rock beds on shoals or along lake shores provided there is good intergravel flow to irrigate embryos (Groot, 1996; Wilson, 1997; Quinn, 2005). Males normally occupy spawning areas before females (Morbey, 2000). Females arrive later and start to explore places to build a series of nests where they deposit their eggs. Females look for pool-riffle transition zones (Gaudemar et al., 2000a) where depth decreases and flow accelerates. A general description of the spawning behaviour can be made following a chronological history from nest site selection to nest completion with the subsequent oviposition, covering of the eggs and in some species nest defense by a female until her death.

Nest selection

Females search for unoccupied spaces in areas with appropriate gravel, water depth and velocity conditions to place their redds (Groot, 1996). They inspect different river stretches while swimming in circles with their lower jaw touching the gravel (personal observations; Figures 6 and 7). Authors have used different names for this exploratory behaviour, i.e. "searching" in Fabricius and Gustafson, 1954; "nosing" in Groot, 1996. During this period, males frequently join females (Figure 8) and depending upon their readiness to spawn, may start to show courtship activities. At this stage, they frequently press their snout against the females' mid body (Berejikian et al., 1997; Figure 9). The purpose of this behaviour seems associated with testing the female's spawning condition, but its actual function is unknown.

Once an area is selected, females turn to one side and "beat" the gravel with rapid thrusts of their tail. These diggings are done from various directions and cover a relatively large area (Gaudemar and Beall, 1999). Frequently, females abandon places where they have dug repeatedly, indicating the exploratory nature this preliminary activity (personal observations). Different terms have been

Figure 6. A chum salmon female searching a location to build her nest.

Figure 7. A chum salmon female searching a location to build her nest.

Figure 8. A *searching* brown trout female accompanied by a male.

Figure 9. Chum salmon male presses his snout against the female's body.

Figure 11. Pink Salmon female digging its nest.

used to name these exploratory diggings (e.g. "random cutting" in Jones and Ball, 1954; "test digging" in Fleming, 1996; "digging with motion" in Gaudemar and Beall, 1999; "exploratory cutting" in Evans, 1994).

Nest building

Once a nest site is selected females switch to more vigorous diggings concentrated in a specific location and performed in an upstream direction (Figures 10–11). Authors have used different names for this kind of digging (e.g. "nest digging" in Tautz and Groot, 1975; "redd cutting" in Evans, 1994; "still diggings" in Gaudemar and Beall, 1999). The change between exploratory and actual nest digging can be used as a point where spawning starts a new phase. At this stage, a

Figure 10. Coho female digging its nests.

cleared elliptical area can be seen from the riverbank with the naked eye provided there is good water visibility.

Several patterns are common among the different species during females' nest building behaviour (the exception is the lake trout (*Salvelinus namaycush*) which spawns without building a nest; Gunn, 1995). From a resting position just slightly downstream from the selected location females slowly swim forward passing over the area. Next, they let the current carry them back to their original position. During this backward movement, they use their caudal, anal and sometimes pelvic fins to touch the gravel (personal observations). Once, in their original location females perform an upstream acceleration turning on to one of their sides and beating the gravel with their tails. Alternatively, females can start a digging episode after circling their nest by actively swimming (this is the rule for females spawning in still waters; see McCart, 1969). The number of tail beats used to build a nest increases progressively, but declines as the nest reaches completion (Tautz and Groot, 1975; Schroder, 1981; Gaudemar and Beall, 1999).

The female's downstroke loosens substrate materials and they are lifted into the water column by her upstroke (Quinn, 2005). Underwater recordings played at slow motion showed how currents carry fine particles loosened by digging downstream. In contrast, gravel can be seen to move forward (upstream) when the tail beats down and backwards when the tail beats up. As a result a depression enclosed in elevated rims is formed

approximately in the middle of the cleared elliptical area. This depression constitutes the pit where eggs will be laid (Burner, 1951; Crisp and Carling, 1989; Edo et al., 2000; Quinn, 2005). Detailed descriptions of digging behaviour for particular species can be found throughout the literature (Needham and Taft, 1934; Jones and King, 1950; Fabricius and Gustafson, 1954; McCart, 1969; Hartman, 1970; Legget, 1980).

After a digging episode, females have two ways to return to the nest. They either turn around and swim or let currents to carry them back. These two manners of performing the same action can be used for predicting how close a female may be to oviposition. The later behaviour occurs more frequently as spawning approaches (personal observations).

In addition to normal digging, female charr perform another nest building behaviour unique to their genus that has been described and named "sweeping" by Fabricius and Gustafson (1954). During sweeping, a female char remains over her nest and continually bends her tail as she undulates her body. As a result of this swimming-in-place action, a jet of water removes sand and other fine materials over their nest. Sweeping is thought to be an adaptation of the *Salvelinus* genus to spawning in still waters and has the function of cleaning fine sediments from nests (Fabricius and Gustafson, 1954).

During nest construction females defend their redd locations from adjacent and newly arriving females (Fleming and Gross, 1994). Prior residence is a good indicator of the ability to hold a territory (Foote, 1990; Morbey, 2002). However sometimes, females are forced to abandon their nest by others (personal observations). In addition, in species spawning in high densities, attacks between neighboring nesting females are common (Quinn, 1999).

Males do not contribute to nest building (but see male digging as a displacement reaction below). Instead, they fight to have access to nesting females (Groot, 1996). Normally, they combine actual fighting with threat displays used to intimidate rivals (personal observations). After prolonged fighting that could last for hours a hierarchy rank is established (Hanson and Smith, 1967; Foote et al., 1997). The dominant male occupies the position closest to the female and spends his time courting her and preventing other males from approaching the female (personal observations). To court her, he approaches the female laterally from a backward position and rapidly shakes (with high frequency and low amplitude) his body from head to tail quivering intensely (Jones and King, 1949; Figures 12 and 13). Quivering is the typical courtship behaviour common to all salmonines and has been extensively discussed in some of the species (Jones and King, 1950; Fabricius and Gustafson, 1954; Legget, 1980). Normally, at the earlier stages the quiverings are almost imperceptible, as the male darts toward the female's lateral side; this behaviour has been named "gliding" by Fabricius, (1953) and "flanking" by Legget (1980). In contrast, the quiverings close to spawning are intense and at times the male will gape (personal observations).

A dominance hierarchy also exists among satellite fish (Hanson and Smith, 1967). Smaller or weaker males are normally forced to the rear or to one side of more high-ranking males (Schroder, 1973). However, this system is not stable and continuous fighting and agonistic displays are required to maintain it (Petersson and Järvi, 1997; personal observations).

Oncorhynchus males may dig during the spawning process (Figure 14; Table 2). However, male digging, instead of being a nest building behaviour, has been considered an aggressive display and several authors have linked it with male–male aggression (Chebanov, 1980; Healey and Prince, 1998; Quinn, 1999). Probably, as anticipated by McCart (1969), male digging is a displacement reaction. Displacement reactions are defined by Wilson (1975) as behavioural patterns with no relevance whatsoever to the circumstance in which the animal finds itself, and have been long discussed in the literature (Tinbergen and Van Iersel, 1947; Tinbergen, 1952; Eibl-Eibesfeldt and Kramer, 1958).

Nest probing

As nest building progresses a female will test its shape and depth by lowering her anal fin into the gravel in a behaviour called probing (Groot 1996; Figures 15 and 16). Other authors have used different terms to name this behaviour (e.g. "anchoring" in Fabricius and Gustafson, 1954; "crouching" in Jones and Ball, 1954). During a probing the female raises her caudal fin, flexing it upwards off the bottom, as a result her anal fin
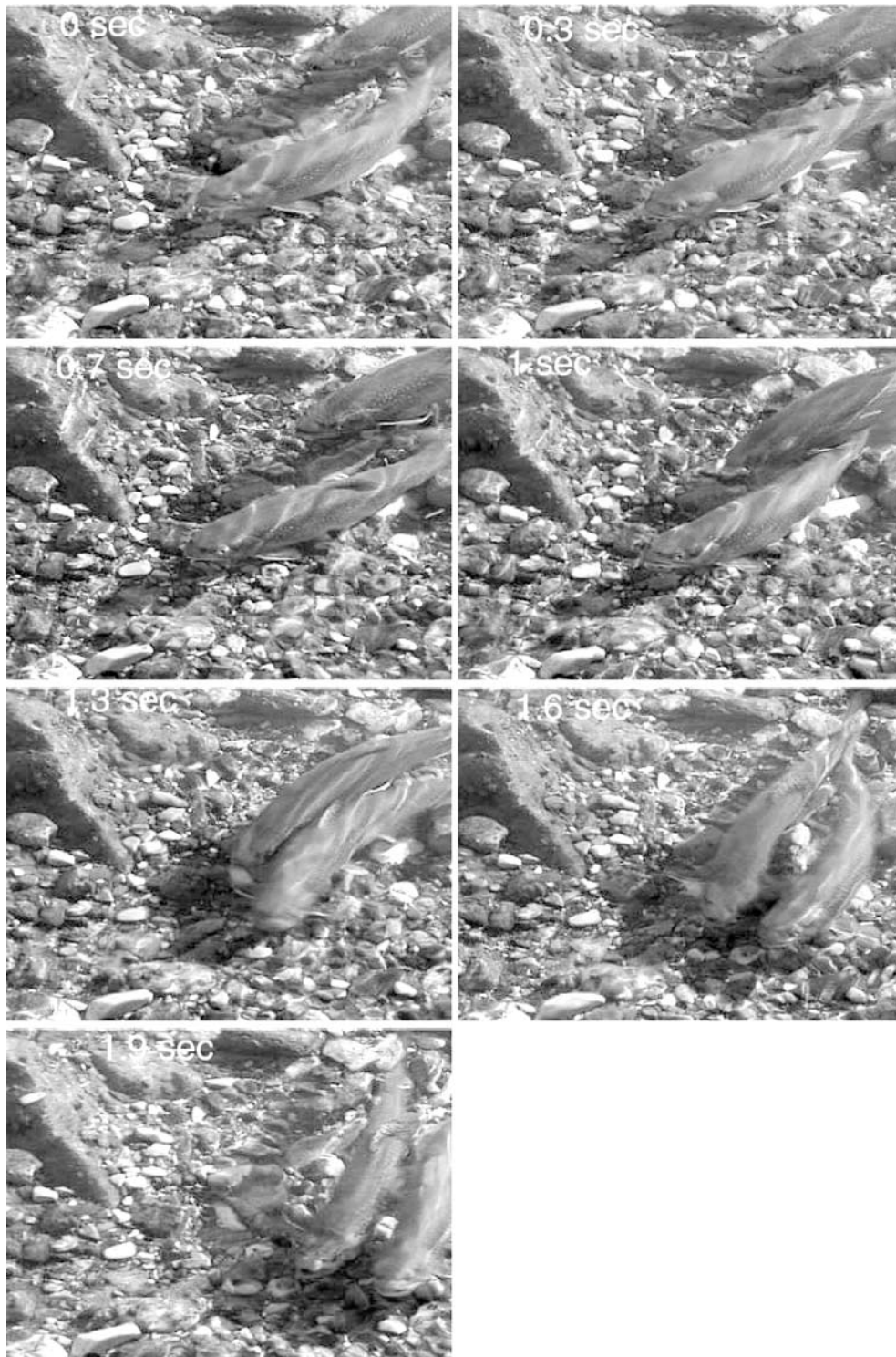
10

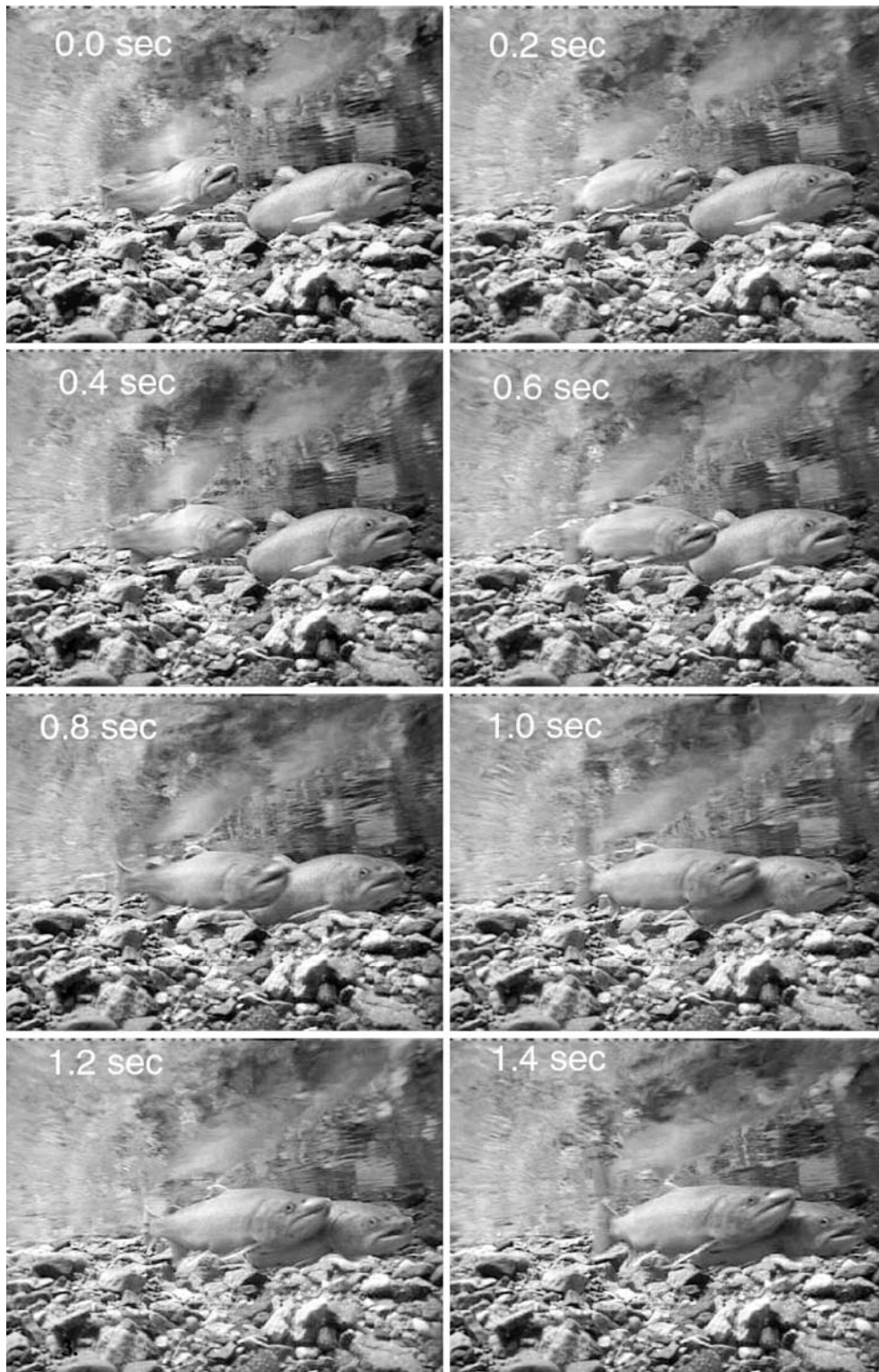*Figure 12.* Video frame sequences showing a brook trout male performing a quivering to a nesting female.

Figure 13. Video frame sequences showing a bull trout male performing a quivering to a nesting female.

Table 2. Presence or absence of male digging in *Oncorhynchus* species

Species	Male digging	References
Rainbo trout	Yes	Berejikian (pers. com.; pers. observations)
Cutthroat trout	–	
Masu salmon	Yes	Yamamoto (pers. com.)
Chinook salmon	Yes	Berejikian (pers. com.)
Coho salmon	Yes	Healey and Prince (1998)
Chum salmon	Yes	Schroder (1981; pers. observations)
Sockeye salmon	Yes	Quinn (1999; pers. observations)
Pink salmon	Yes	Heard (1972; pers. observations)

Figure 16. Details of a coho salmon female *probing* her nest. Observe in this picture how the anal fin is pressed deeply into the gravel.

Figure 14. Sockeye salmon male digging behaviour.

Figure 15. Details of a coho salmon female *probing* her nest.

remains pressed into the gravel and her full body lays in an angle within the nest depression (personal observations). It has been documented that females also use their pelvic and caudal fins to assess nest readiness (Hartman, 1970). During a female's probing phase the frequency of digging decreases (Tautz and Groot, 1975) and the female spends more time lying within her nest (personal observations).

Female probing is a signal for males that oviposition is getting closer (Jones and Ball, 1954). As a result, the frequency of courting and fighting behaviours increases (Tautz and Groot, 1975; Gaudemar and Beall, 1999). The dominant male responds to probings with quiverings (Legget, 1980; Satou et al., 1994; Berejikian et al., 2000; Gaudemar et al., 2000b). At the same time he guards her from other males (personal observations). To do so he maintains a backward position and constantly passes over her caudal peduncle from side to side trying to guard her from males coming from either side. This conduct has been called "crossover" (Tautz and Groot, 1975; Berst et al., 1981; Berejikian et al., 1997; Gaudemar et al., 2000b). Crossover behaviour possibly contributes to courting due to constant stimulation of the female's dorsal area (personal observations). When another male approaches the spawning pair, the dominant male will invariably place his body between the female and the encroaching male while maintaining an threatening posture (personal observations). If this does not deter the new male, the courting male will either directly attack his rival (chasing and biting) or initiate an

escalating series of threatening displays (Fleming 1996; Healey and Price, 1998).

Published descriptions have portrayed different types of threatening displays that vary in intensity and possible significance (Table 3). In addition, there are species-specific displays and when similar threats are used by different species they may be performed differently (Esteve, 2005). Sometimes a secondary male will respond to a threatening display with another one. A satellite or newly arrived male often approaches the spawning pair from the back. The dominant male moves towards him while performing a lateral display (Figure 17). The secondary male adopts a lateral display posture and both fish swim parallel to one another for a short period of time. If the action persists the dominant male will most likely launch a direct attack or display in a "T" formation (Figure 18; Schroder, 1981). Conversely, if the newcomer moves downstream or away from the pair, the dominant male will often perform flanking (Figure 19) and/or tail displays (Figure 20) to drive him off (Esteve, 2005).

Nest completion and oviposition

As the nest nears completion it gets deeper and consequently the female's body angle during probing behaviour increases. When this angle reaches approximately 20° the nest is complete (Tautz and Groot, 1975). From this moment oviposition may proceed at anytime. Several other signs, common to all the species indicate that oviposition is imminent. As spawning nears females probe more and dig less (Tautz and Groot, 1975; Gaudemar and Beall, 1999). This change in digging and probing frequencies is accompanied by a noticeable increase in a female's respiratory frequency (personal observations). Female movements in the minutes before oviposition are slower. At this stage, it is common to observe the emission of bubbles through the female's gills (Figure 21). This behaviour is also seen in males and it may be a "comfort" behaviour (Tinbergen, 1951; Schroder, 1981). Alternatively, the emission of bubbles may be a buoyancy adjustment, as during oviposition females need to be close to the substrate (Hartman, 1970).

According to my observations, probing activity immediately before spawning lasts longer and many times the female will partially gape while probing (Figure 22). Finally, seconds before spawning, the female will start vibrating her body while probing and gaping. At this moment, females may sometimes perform a false spawning (Figures 23 and 24; Jones and Ball, 1954; Petersson and Järvi, 2001; Esteve, 2005). During false spawning, the female imitates a real spawning (probing, gaping and vibrating), but does not expel eggs. The dominant male and sometimes other secondary males join her adopting the spawning posture and on some occasions they will emit sperm (personal observations). Apparently, false spawnings are low intensity behaviours produced when females, at the last moment, do not receive enough stimuli (from their nest shape or from their mate) for oviposition (Jones and Ball, 1954; Esteve, 2005). During a successful spawning both fish emit their gametes while gaping and vibrating with their bodies pressed together and their fins fully extended. Their caudal fins remain flexed upwards forcing their vents into the substrate (Figures 25 and 26). The spreading of pelvic and ventral fins plus gaping possibly helps the pair to remain in a stationary position over the nest (Greeley, 1932). According to my observations, female and male spawning vibration movements differ from the courtship quivering performed by males. They are confined to their lower body mid-section, they have lower frequency, and they are often interrupted for short intervals. When false and true spawning events occur subordinate males, as well as sneaker males, frequently join the pair to release sperm. This phenomenon can occur at the same time the dominant male is spawning (Figures 27 and 28) or immediately afterwards (Figure 29). After true spawning events females immediately perform a series of rapid and characteristic digs. A fundamental behavioural difference exits between female charr and females in the genera *Salmo* and *Oncorhynchus*. Typically, charr females have successive spawning events (1–5) in a single nest separated by only a few seconds or minutes (Armstrong and Morrow, 1980; Johnson, 1980; Kitano et al., 1994). Conversely in the other two genera, females lay only one batch of eggs per nest (Leggett, 1980; Johnson, 1980).

Nest covering

After releasing their eggs *Oncorhynchus* and *Salmo* females immediately cover them with a rapid series

Table 3. Common fighting displays performed by Salmoninae males during the spawning process

Displays	Description	References
Frontal display	The head is down and the tail is up. The dorsal fin is depressed (similar to a bottom feeding posture)	Fabricius (1953), Power (1980), Buttler (1991), Fleming (1996)
Lateral display	A fish lies in parallel to its opponent with its body flexed upwards and the fins erected	Jones and Ball (1954), Newcombe and Hartman (1980), Järvi (1990), Buttler (1991)
T-display	From a lateral display, the fish swims upstream and turns its body presenting it to the opponent in a 90^0 angle and letting the current move it towards its rival	Schroder (1981), Groot (1996)
Flanking display	The dominant male lets the current to carry its body towards the opponent presenting his body flank in an angle while maintaining the fins erected and the body flexed (lateral display)	Esteve (2005)
Tail display	The dominant male with the fins erected and the body flexed (lateral display) flaps his tail forcing water, over his opponent's head	Jones and King (1950), Fabricius and Gustafson (1954), Buttler (1991), James and Sexauer (1997)

of discrete digs (Figure 30). The first few covering digs are very gentle and normally do not move any gravel (personal observations). They have the apparent function of gently locating the released eggs into the interstitial spaces of the nest. Coverings digs are markedly different from those used to build nests. Apart from their greater frequency and lower number of tail beats, they are performed laterally from the upstream rim of the nest (McCart, 1969; Hartman, 1970; Keenleyside and Dupuis, 1988a; Quinn, 2005). Additionally, during a covering dig females do not curve their mid-body; instead most of the bending occurs in their caudal peduncle (personal observations). Eggs are usually completely buried, by a depth of gravel equal to the depth of a nest within 30–40 minutes following spawning (McCart, 1969).

Salvelinus females perform a unique behaviour after spawning consisting of a slow and rhythmic swinging of the body. This undulating apparently functions to disperse recently deposited eggs into the crevices of a nest and possibly to aerate them (Needham and Vaughan, 1952; Fabricius and Gustafson, 1954; Needham, 1961; Martin and Olver, 1980; Power, 1980; James and Sexauer, 1997). Undulating is a similar, but more intense, behaviour to sweeping described at the nest building stage and again is probably an adaptation of *Salvelinus* to spawning in still waters (Fabricius and Gustafson, 1954). During the nest-covering

Figure 17. Sockeye salmon male performing lateral display to another male in his left side.

Figure 18. A chum salmon male is attacked while performing a T-display.

Figure 19. Brook trout male (foreground) in *flanking display* to a male in dorsal display.

Figure 20. Brown trout male in tail display to a male in the rear; the most backward fish is the female.

Figure 21. Atlantic salmon female emitting bubbles through her gills.

Figure 22. Chum salmon female gaping during a probing.

Figure 23. Coho salmon pair during a false spawning.

Figure 24. Atlantic salmon pair during a false spawning.

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Figure 25. Chum salmon spawning act.

Figure 26. Sockeye salmon spawning act.

Figure 27. Pink salmon *multiple paternity* spawning event.

Figure 28. Sockeye salmon *multiple paternity* spawning event.

Figure 29. Two Atlantic salmon males release sperm in the nest some seconds after the female has spawned with the dominant male.

Figure 30. A Chum salmon female covers her nest by digging.

phase, dominant males move away from the female and begin searching for other spawning opportunities. Satellite males, however, will often court a recently spawned female (Berejikian et al., 1997; personal observations). Dominant males (when there are no other females available) sometimes remain in the redd attending the spawned female (personal observations). This may occur because as the spawning season progresses females become relatively scarce or the ones left are normally already guarded by other males.

Once the process of covering is done, females may rest for a period of time or immediately start to dig a new nest. The new nest is usually located upstream from the previous one and the last covering diggings are used to start it (Groot, 1996). Semelparous species use only one redd which they defend until death (but see Bentzen et al., 2001). In contrast, iteroparous species sometimes use two or more redds to locate their nests (Barlaup et al., 1994). In addition, semelparous species normally remain on their redds during the entire spawning process, whereas iteroparous females leave redds for periods of time during and after nest building (personal observations).

A few studies have been able to follow the complete, or partial, spawning history of different salmonines in controlled areas (Table 4). This has lead to a better understanding of the entire process. The tremendous variation found in the length of time during which females complete their spawning activity has not yet been explained.

Recommendations for future research

Despite the vast amount of work done with salmonines, a complete understanding of their mating behaviour has not been achieved. Three main problems are apparent. First, there are many fish species whose spawning behaviour has been poorly studied. Literature exists on the breeding behaviour of the main species within the three better-known genera (*Salmo*, *Salvelinus* and *Oncorhynchus*), but spawning research has substantially favoured Atlantic salmon and the five Pacific salmons present in North American rivers. Furthermore, there are virtually no references about the breeding activities of some of the rare *Oncorhynchus* salmonines found in western areas of the Southern USA and Northern Mexico (but

Table 4. Spawning history of different Salmoninae species

Ovip. T	n_d	n	T_i	T_n	Species	References	Particularities
3.5 hours	250–300	8	3–4 hours	–	Atlantic salmon	Jones and King (1949)	The data are from one single female
–	–	–	4–37 hours	3 days	Sea trout	Evans (1994)	Observations were recorded on the wild
–	–	up to 14	4 hours–9 days	–	Atlantic salmon	Fleming (1996)	
1 hour–2 days	–	–	–	5-6 days	Atlantic salmon	Fleming (1998)	
–	–	6–11	9.17 hours	4 days	Atlantic salmon	Gaudemar and Beall (1999)	Size-matched pairs were allowed to spawn in absence of competition
2.7–7.2 hours	–	–	–	–	Brook trout	Blanchfield and Ridgway (1999)	Ovip. T. was shorter when females paired with larger males
–	–	2–6	9.6–16.1 hours	–	Chinook salmon	Berejikian et al. (2000)	T_i was shorter when females were paired with larger males.
5 hours	300–340	–	3 –7 hours	–	Chum salmon	personal observations	Observations were recorded on the wild. The data are from one single female

Ovip. T (oviposition time): time from nest initiation until oviposition; n_d (number of diggings): number of digging bouts per nest; n: number of ovipositions per female; T_i: time interval between two ovipositions; T_n: total nesting time (does not include the time of redd defense after the last oviposition).

see Rinne, 1980; and Knapp and Vredenburg, 1996). The spawning behaviour of members of other genera such as *Brachymystax*, *Hucho*, and *Salmothymus* remains largely unknown. Second, except for a review by Stearley (1992) concentrated on the genus *Oncorhynchus* and a summary discussion by McLennan (1994), there are no studies where the behaviours among the different species are compared in an evolutionary sense. Third, a thorough discussion of two proposed mechanisms of sexual selection in salmonid spawning behaviour, i.e. Fisherian runaway selection (Fisher, 1930 and 1958) or the *good taste* model and Zahavi's handicap principle (Zahavi, 1975; Zahavi and Zahavi, 1997) or *good genes* model, needs to be discussed in relation to different salmonid species.

Acknowledgements

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