Salmoninae Spawning Behaviour

2. Salmoninae Spawning Behaviour

Introduction

Homing fidelity to natal spawning grounds and nest building behaviour have made salmonines an ideal target for behavioural studies. Pioneer work by Jones & King (1949, 1950 & 1952) with Atlantic salmon, Jones & Ball (1954) with brown trout and Atlantic salmon, and Fabricius (1953) and Fabricius & Gustafson (1954) with arctic charr described in detail the breeding patterns in these species. These works were based on extensive observations in aquaria and semi-natural channels. Live observations were supported with underwater film recordings for further analyses. As a result behavioral patterns during spawning were described and hypotheses about their likely adaptive value were presented.

Recently other authors have investigated the spawning behaviour of some Salmoninae members in different detail (Chebanov, 1980 for pink salmon; Newcombe & Hartman, 1980 for rainbow trout; Leggett, 1980 for dolly varden; Schroder, 1981 & 1982 for chum salmon; Foote, 1987 for sockeye salmon; Sigurjónsdóttir & Gunnarsson, 1989 for arctic charr; Evans, 1994 for sea trout; Fleming, 1996 for Atlantic salmon; James & Sexauer, 1997 for bull trout; Healey & Prince, 1998 for coho salmon; Blanchfield, 1998 for brook trout; Berejikian et al., 2000 for chinook salmon; for a more detailed review see Fleming, 1998). Other scientists have discussed different aspects of the salmonines breeding ecology (Beacham & Murray, 1985 for morphological differences in spawning Pacific salmon across latitude; Foote, 1988 for male choice in kokanee and sockeye salmon; Crisp & 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 populations have declined and hatcheries 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 from hatchery fish escaped into the rivers (Fleming & Gross, 1993; Fleming et al., 1996; Berejikian et al.,. 1997; Petersson & Järvi, 1997; Chebanov & Riddell, 1998; Fleming & Petersson, 2001).

Despite this tremendous work a comparative detailed description of the spawning behaviour observed in the wild and following a similar protocol is still needed. This chapter is an attempt to cover this gap. It explains in an integrated and comparative way how this group of fish behaves during reproduction.

Methods

Remote Underwater video

Hi-8 mm and mDV video cameras mounted in acrylic underwater housings were used to monitor spawning Salmonids in the wild and in semi natural spawning channels.

The recording protocols went as follows: the camera was placed in the river remaining motionless at 1-0.3 meters from a developing salmonids redd (**Figures 1, 2 & 3**). The video and audio signals were taken out via cable to an mDV digital video cassette recorder with a color monitor (Sony GV-D900E). Recordings of the live picture were done from outside the river using a remote commander (Sony RM 95) that allowed zooming and focusing manually.

All the used cameras were provided with angular lenses (x 0.5) and shutter speed was 25 frames sec-1 (PAL).

Figure 1. A camera inside an acrylic housing attached to a rope records a brook trout female on a redd.

Figure 2. A camera inside an acrylic housing records a spawning pair of chum salmon.

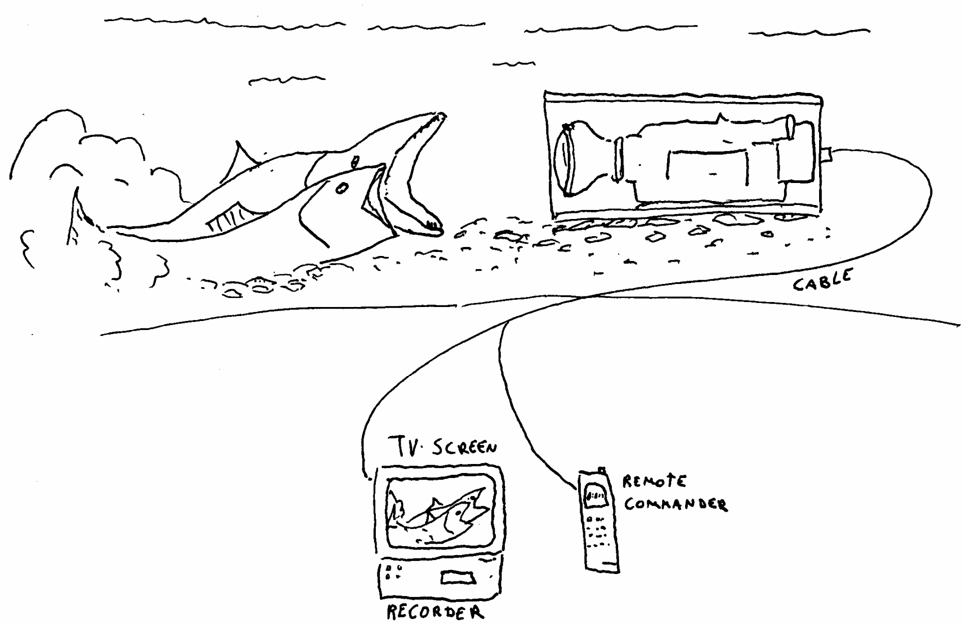


Figure 3. Diagram showing the remote underwater video settings.

According to my experience the camera presence does not disturb the fish natural behaviour. Normally, fish will completely ignore it as if it were any natural object on the river bottom. When fish are motivated to spawn they will return only some seconds or a few minutes after leaving the camera submerged.

For night recordings a monochrome CCD high sensitivity CCTV camera inside a waterproof housing was used (Sony M-370, 3.5 mm lens). A 12-V 900-watt power light with an infrared (800 nm) filter was used to illuminate the salmon redds in complete darkness without disturbing natural behaviour (Gaudemar & Beall, 1999; Grant et al., 2002).

The discussion is based in over 1500 hours of observations during spawning in a 10 year period and resulted in over 300 hours of recording tapes of different species (**Table 1**).

Table 1. Approximate numbers of recording hours and nesting females of different salmonid species used in this study.

	number of recording hours	**number of nesting females**
Arctic grayling	11	9
Atlantic Salmon	40	16
Brown trout	30	14
Dolly Varden*	5	2
Brook	30	7
Bull*	6	4
Cutthroat	3	0
Steelhead*	30	9
Chinook*	10	10
Coho	25	11
Sockeye	55	33
Chum	50	19
Pink	10	9
Total	**309**	**143**

(*) Recordings from other scientists are included

Tape analysis

The tapes were analyzed individually registering the time code for the following behaviors: *quiverings, diggings, attacks, fighting displays, probings, false spawnings* and *spawnings*. These and other less common behaviors, which were also noted, are discussed below. After analyzing and timing, edited tapes were made showing the most significant behaviours for each of the species. Tapes showing the same behaviour pattern in different species were also edited (e.g. female digging). Behaviours were then compared using frame-by-frame and slow motion video playback of tapes.

To test different hypotheses each underwater tape was treated as an independent sample of one hour of spawning activity (**Chapters 3 & 4**). However, behaviour changes as nest development progresses (Gaudemar & Beall 1999). To control for this only tapes pertaining to the same spawning phase were used (see **Table 4**). Equally, to control for fish size tapes with a similar ratio of female-male size were used.

Locations and dates

Underwater recordings were done during a ten-year period in a number of rivers and spawning channels across Europe and North America (**Table 2**). Particularities (notes) found are also included and constant references to them will be made during the discussion.

Table 2. Spawning observations in time, location and species. Behaviours noted during live observations and after tape reviewing are reported.

Location river, region, country	**Date**	**Species**	**Notes**
Cares Asturias, Spain	Dec.1993	Atlantic salmon (*S. salar*)	Observations of adults attacking precocious parrs. Interspecific courtship (sea trout males to Atlantic salmon females).
Vall Ferrera Pyrenees Mountains Spain	Nov.1995	Brown trout (*S. trutta*)	Evidence of male choice and female-female competition. Attacks of males on females. Female nest replacement. Changes in the hierarchy ranking. Lateral display lowering the jaw. Tail displays. Flanking displays. Observations of adults attacking parrs. Male-male quiverings in an agonistic context.
Pigueña Asturias, Spain	Dec. 1995	Atlantic salmon	Female digs without a male. Male performing a prolonged quiver away from a female. It was similar to the *violent quivering* done by other salmonines species. Series of quiverings separated by 3-4 seconds similar to the ones performed by trout and charr.
Farrar Highlands, Scotland	Nov-Dec. 1996	Atlantic salmon	Adult male quivering to the underwater camera. The late afternoon and the dark hours were the times with most spawning activity. Exploratory diggings. False nests. Females spend hours away from the nests. Attacks from adults of both sexes to precocious parrs. Attacks between precocious parrs when adults are absent. Noticeable differences among precocious parrs size.
Cares Asturias, Spain	Nov. 1997	Sea trout (*S. trutta*)	Small male courting a big female. Female exploring behaviour. Lateral display lowering the inferior jaw.
Dobra Asturias, Spain	Dec. 1997	Sea trout	Violent quiverings released in a fighting context. A trout female has dug the gravel on two occasions during an attack indicating a displacement digging similar to the ones present in *Oncorhynchus*.
Cares Asturias, Spain	Dec. 1997	Sea trout	Exploring. Series of quiverings separated by 3-4 seconds. Females attack small males. Gradual transition between fighting to courtship behaviours.
Nansa Cantabria, Spain	Dec. 1997	Atlantic salmon	Precocious parr quivering to adult female. Adult male quivering to the underwater camera. Satellite males take advantage of dominant male's absence to court a female. During probing a female oscillates her anal fin inside the gravel. Satellite males release sperm without the female present. False spawning. Precocious parr darts into the nest while adults spawn. Spawning trembling differs from males' quivering.

Table 2. (continued)

Location	Date	Species	Notes
Vall Ferrera Pyrenees Mountains Spain	Nov. 1998	Brown trout	Observations of male's choice: attacks from males to females. Female nest replacement. Series of quiverings separated by 3-4 seconds.
Cares Asturias, Spain	Dec. 1998	Atlantic salmon	Adult male quivering to the underwater camera. Interspecific quiverings (sea trout male-Atlantic salmon female).
Findhorn Highlands, Scotland	Oct-Nov. 1999	Atlantic salmon	Adult male quivering to the underwater camera. Most spawning activity during dark hours. Homosexual quiverings. Interspecific courtship (male trout-female Atlantic salmon). Precocious parr eating eggs. Male defends the territory without the female present. Satellite males courting a recently spawned female. Possible hybridization between Atlantic salmon and brown trout.
Cares Asturias, Spain	Dec. 1999	Atlantic salmon	Homosexual and interspecific quiverings (sea trout male-Atlantic salmon male). Displays and attacks between precocious parrs. Male defends the territory in the redd without the female present
Cedar Washington, USA	Oct-Dec 2000	Sockeye salmon (*O. nerka*)	False spawnings. The female spends time over her nest with her caudal fin folded to a lateral extreme (flexing). Male tastings. Female passive quiverings. Female displacement diggings. Male and female displacement diggings not associated with the presence of other fish, induced by the use of a light beam during dark hours. Differences in male colouration. Female mimics. Digging sound releases attacks between neighboring females. A female "probes" the nest to test the eggs covering.
Chehalis British Columbia Canada	Feb-Mar. 2001	Coho salmon (*O. kisutch*)	Continuous attacks from focal females to males. Most of the attacks are directed to small males. Diggings are more intense than the ones seen before with other species. False spawnings. Sperm competition during the spawning of one female with 8 males. Female forced to abandon her nest by another female. Females spend time away from their nests.
Skykomish Washington, USA	Sep. 2001	Pink salmon (*O. gorbuscha*)	Female exhibits choice by attacking undesirable males. Female displacement digging. Male gliding behaviour. Diggings end with the female in a vertical position; the quiverings are short in frequency and large in amplitude. Digging sound releases attacks between neighboring females.
Weaver Creek B.C. (Canada)	Oct. 2001	Pink salmon	Different male coloration according to the hierarchy status. Female displacement digging. Female passive quiverings. Sperm competition at the spawning act. *Flexing* and *winding* behaviour.

Table 2. (continued)

Location	Date	Species	Notes
Big Beef Creek Washington (USA)	Nov-Dec 2001	Chum salmon (O. keta)	Female displacement diggings. T-displays. Homosexual quiverings. Attacks from males to females (male choice). Females use their inferior jack to taste the substrate quality (exploring). Males use their nose to taste female's abdominal cavity (tasting). In some of the quiverings the male will use his head and physically hit a female's belly. Frequent sperm emissions associated to the presence of a high number of males around a female. Secondary chum males use a "female mimic tactic". Digging sound releases attacks between neighboring females.
Big Beef Creek Washington, USA	Nov-Dec 2001	Coho salmon	False spawnings. Female *flexing* behaviour. Adults "allow" cutthroat trout to eat their eggs. Violent quiverings. Female stays over the nest moving her caudal fin to both extremes without progressing (*winding).* Possible hybridization between coho female and cutthroat male.
Steep Creek Alaska, USA	August 2002	Sockeye, & Chinook salmon (*O. tschawytscha*)	Female chinook probe their nest by swimming over it and using their pelvic, anal and caudal fins to test it (*passing-probing)*. Chinook female spends time away from her nest. Tail-beat display. Female was observed performing digs without a male present. Interspecific spawning between a chinook female and a sockeye male. Non-dominant male displacement diggings.
Yakima Wa, USA	Sep. 2002	Chinook salmon	Male doing incomplete (low intensity) quiverings to a salmon stationary dummy.
Sauk SF River Washington, USA	Oct. 2002	Bull trout (*S. confluentus*)	Female digs release violent quiverings. During violent quivering the male raises his head and extends his gills. Violent quiverings takes place away from the female. The male courting intensity (measured in quiverings/minute) is higher than in the other Salmonines; quivering also lasts longer. Bull trout females have a particular way of probing by which they lay motionless in the substrate with their body fully extended but not in an arching position. The dorsal fin also stays extended during this behaviour (*lying)*. *Flexing* behaviour. As oviposition comes closer the frequency of attacks increases. Adults attacking parrs. A variation in quivering quality within the same male can be noticed by means of time duration and intensity. Female remains for long time lying in the nest bottom

Table 2. (continued)

Location	Date	Species	Notes
Hell Roaring Creek Montana, USA	Oct. 2002	Brook trout (*S. fontinalis*)	Females *exploring*. Males (sometimes) establish territories and defend then without a female being present. Male *gliding* behaviour. Females spent time away from their nests. The quiverings are very high in frequency and low in amplitude. *Lateral display* lowering the inferior jaw and with pelvic fins vertically extended pointing downwards. *Tail-beat* display. *Flanking display*. Males quiver females even when they are away from their redds. Homosexual quiverings. Very high courting intensity similar to bull and brown trout. Female gaps while digging. Observations of adults attacking parrs. Some parr occupy hidden refuges away from the nest. Females attack to satellite males. Darker colours in males appear to be associated to dominance.
Big Beef Creek Washington, USA	Dec. 2002	Coho salmon	Females spent time away from their nests. Female forced to abandon her nest by another female when she was getting ready to spawn (female nest replacement). *Flexing* behaviour. Violent quiverings. Male quivers female away from the redd.
Cedar Washington, USA	Jan. 2003	Sockeye salmon	Male digs not associated with fights and similar to nest building diggings (sexual displacement diggings). Exploring behaviour. The female turns into one of her sides against the bottom and passes her nest touching it with her pelvic fin (*swinging*). *Flexing* behaviour. A vibratory dummy imitating a spawning female elicited 49 sperm emissions by different males.
Red Rod Creek Montana, USA	May 2003	Grayling (*T. arcticus*)	During quivering the male is normally in a more upstream position than the female. Both fish perform a lateral movement while slightly being carried downstream by the current. The male tilts his body towards the female. Quiverings last longer, have greater amplitude and smaller frequency when compared to the other Salmonids. During spawning the male tilts his body towards the female and covers her with his dorsal fin. Both stay in the same point without progressing upstream or downstream. Territorial males frequently depart in search of females. *Lateral, flanking, tail beating* and *T displays*. Male-male quiverings in an agonistic context.
Marx Creek Alaska, USA	Sep 2003	Chum salmon	The dominant male stays with female after spawning. Female-male behaviours on the second and third egg depositions are less coordinated. Non-dominant male displacement diggings.

A general description of Salmoninae spawning behaviour

Natural selection in terms of offspring production and sexual selection in terms of mating success has shaped the breeding behaviour of Salmoninae subfamily members (Fleming & Gross, 1994; Fleming, 1998; Quinn, 1999). The result has been some common general patterns in the species members (Groot, 1996).

Salmonines spawn in clean cold well-oxygenated waters with gravel bottoms free of silt. 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 successively deposit their eggs. They look for pool-riffle transition zones (Gaudemar et al., 2000a) where depth decreases and water accelerates. Alternatively, some species use still waters provided there is good intergravel flow through upwelling currents (Groot, 1996 for brook trout).

A general description of the spawning behaviour (based on what a human observer would see through an underwater screen) 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 (**Table 6**).

Nest Selection

To select nesting areas females perform a behaviour I call *exploring.* During exploring, they search for unoccupied spaces in areas with appropriate gravel, water depth and velocity conditions. They inspect with noticeable eye and head movements different river stretches while swimming in circles with their lower jaw touching and sensing the gravel (**Figures 4 & 5**; **Table 2**).

During exploring, males frequently join females (**Figure 6)** and depending upon their readiness to spawn, may start to show some courtship activities. At this stage, they frequently press their snout against the females' mid body. This behaviour, I refer to as *tasting,* and it presumably is a way for males to asses the spawning readiness of a female. It may also increase a female's motivation to spawn (**Figure 7**).

Figures 4 & 5. A chum salmon female *exploring* the river bottom.

Figure 6. An *exploring* brown trout female accompanied by a male.

Figure 7. Chum salmon male *tasting* a female

Exploring leads females to choose areas to place their nests (as long as such places are not occupied by other, contemporary females that have established territories). However, in order to definitively select an actual nesting place females need to dig the gravel. This they do by turning to one of their sides and 'beating' the gravel with rapid thrusts of their tail. These diggings are done from various directions and cover a relatively large area (Gaudemar & Beall, 1999 for Atlantic salmon). Frequently, females abandon places in where they have been repetitively digging (**Table 2** for Atlantic salmon), indicating the testing function these primary *exploratory diggings* have.

Nest building

As time progresses, females switch to more vigorous diggings concentrated in a specific location and performed in an upstream direction (**Figures 8-9**). This change between *exploratory* and *building diggings* could be used as a point where spawning starts a new phase (**Table 6**). At this stage, an elliptical area, cleared by the tail beats can be noticed from the riverbank by a human observer's naked eye (provided there is good water visibility).

Figures 8 & 9. Coho (upper left), pink (upper right), sockeye (lower left) and Atlantic salmon (lower right) females digging their nests.

Several patterns are common among the different species during females' nest building behaviour (the exception is the lake trout which spawns without building a nest; Gunn, 1995). From a resting position just slightly downstream the selected location females slowly swim forward passing over the area. Next, they let the current to carry then back to their original position. During this backward movement, they use their caudal, anal and sometimes pelvic fins to touch the gravel as a manner of sensing the bottom and possibly to monitor the building progress. Once in their original position they perform an upstream acceleration turning to one of their sides and starting to beat the gravel with rapid flexures of their tail. Alternatively, females can start a digging episode after circling their nest by actively swimming. The number of tail beats on each digging bout varies between 1 and 16 depending on the species, the nest progression and the females spawning condition. Normally, exploratory diggings are performed with fewer tail beats than building ones. In addition, the number of tail beats (within building diggings) first increases until reaching a maximum some minutes before oviposition (60-30) and then progressively declines as the nest reaches completion (Schroder, 1981 for chum salmon; Gaudemar & Beall, 1999 for Atlantic salmon; personal observations for sockeye, coho and pink salmon).

After digging females almost always return to the nest. To do so, 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, being the later behaviour more common as spawning gets near (**Table 6**).

Underwater recordings played at slow motion showed how currents carry fine particles loosened by a digging bout 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.

In addition to normal building digging female charr perform another nest building behaviour unique to their genus that has been described and named *sweeping* by Fabricius & Gustafson (1954). During *sweeping* a female charr remains over her nest and continually bends her tail and 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.

During nest construction females defend their redd locations from adjacent and newly arriving females. Prior residence is a good indicator of the ability to hold a territory. However sometimes, females are forced to abandon their nest by others (**Table 2** for brown trout and coho salmon). In addition, in species spawning in high densities attacks between neighboring nesting females are common. More detailed digging behaviour descriptions for particular species can be found in the literature (Needham & Taft, 1934 for steelhead trout; Jones & King, 1950 for Atlantic salmon; Fabricius & Gustafson, 1954 for arctic charr; McCart, 1969 for sockeye and kokanee salmon; Hartman, 1970 for rainbow trout; Legget, 1980 for dolly varden).

Males do not contribute to nest building (but see male digging as a displacement reaction p. 36 below). Instead, they fight to have access to nesting females. Normally, they combine actual fighting with threat displays used to intimidate rivals. After prolonged fighting that could last for hours a hierarchy rank is established. The dominant male occupies the position closest to the female and diverts his time in courting her and in preventing other males from approaching the female. To court the female, he approaches her laterally from a backward position and rapidly shakes (with high frequency and low amplitude) his body from head to tail in a behaviour known as *quivering* (**Figures 10 & 11**). There are differences in quivering intensity as the spawning sequence progress. Normally, at the earlier stages the quiverings are almost imperceptible. In those instances the observer can just see males dart into 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 many times the male will gape while performing those. *Quivering* is the typical courtship behaviour common to all salmonines and has been extensively discussed in some of the species (Jones & King, 1950 for Atlantic salmon; Fabricius & Gustafson, 1954 for arctic charr; Legget, 1980 for dolly varden, discussed in **Chapter 4** below).

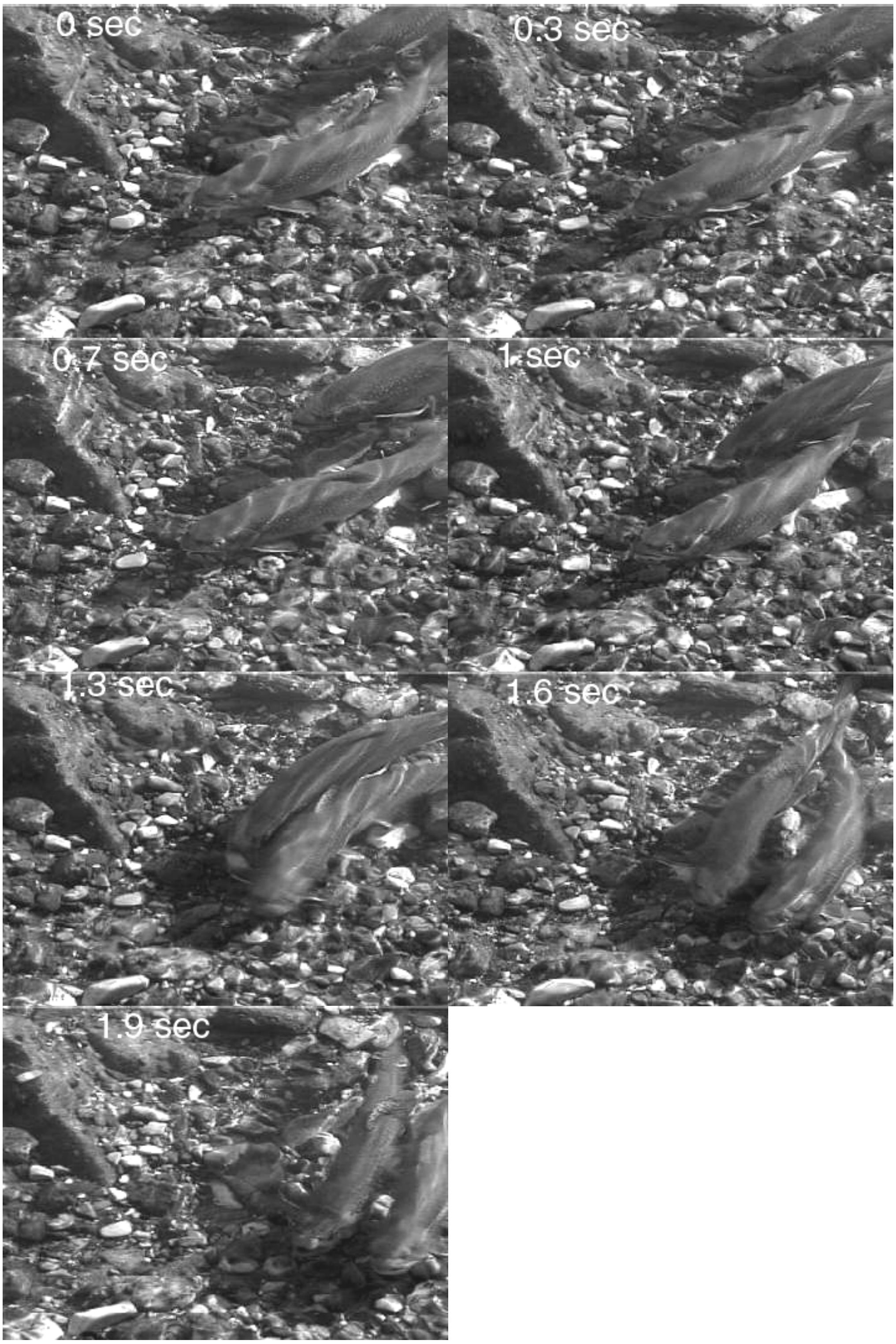


Figure 10. Video frame sequences showing a brook trout male performing a quivering to a nesting female.

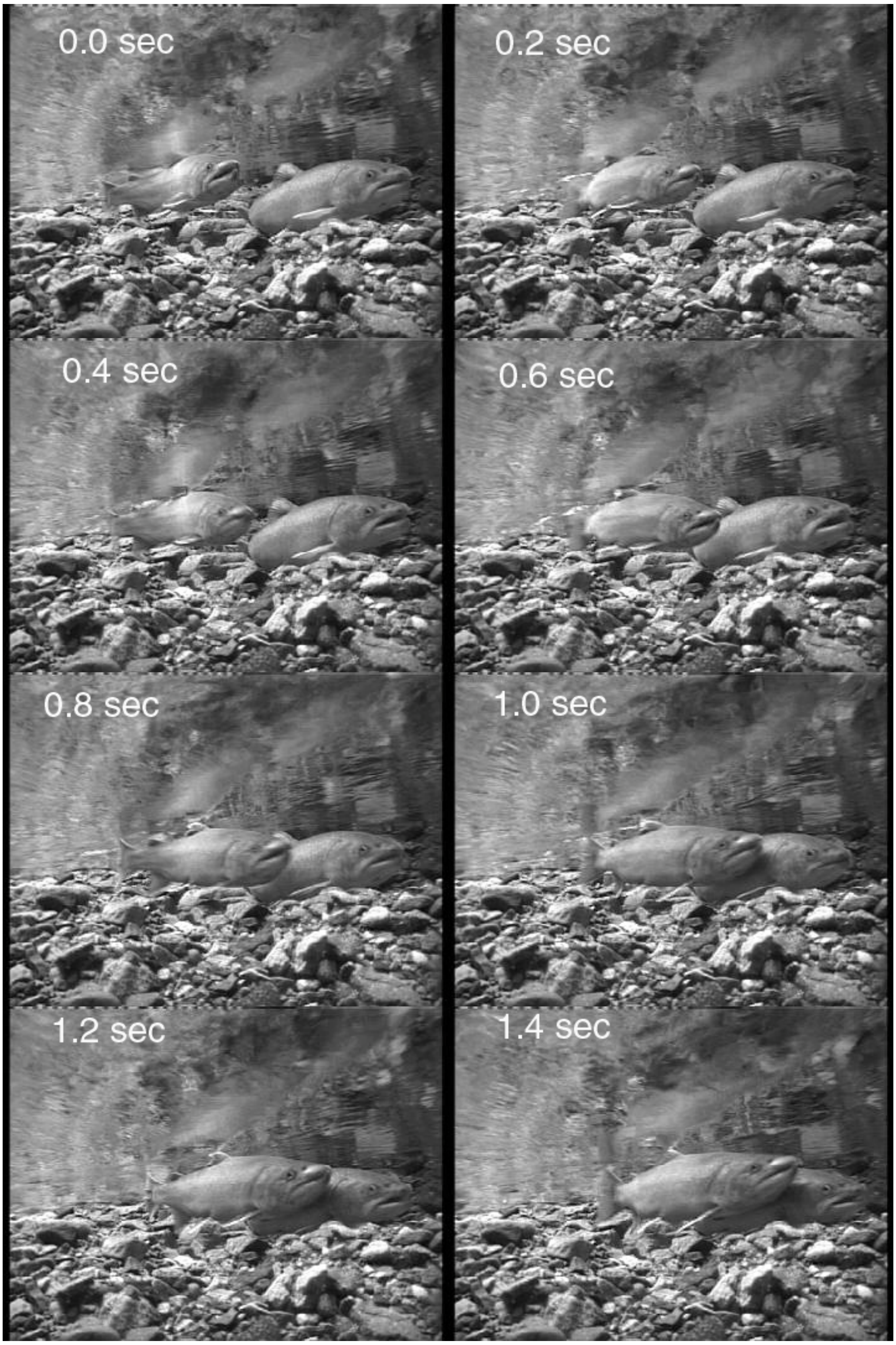
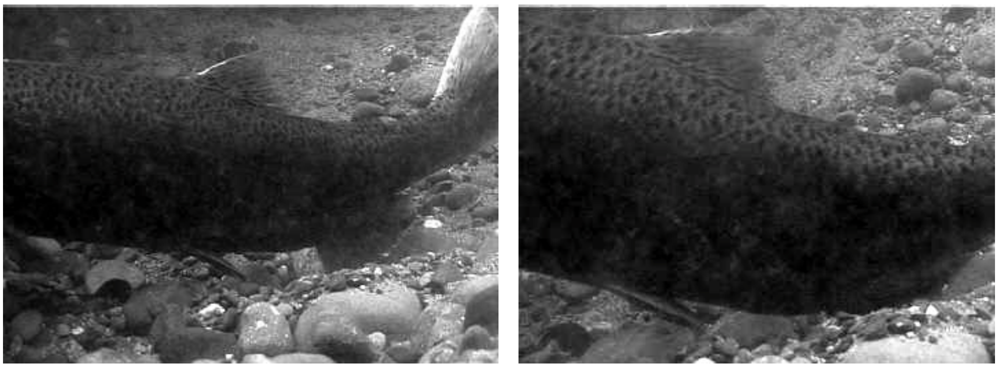


Figure 11. Video frame sequences showing a bull trout male performing a quivering to a nesting female.

Non-dominant males occupy a more backward or lateral position respect to the female, and wait for any chance to approach her. Within these *satellite* fish a dominance hierarchy also exists. Smaller or weaker males are normally forced to the rear, and to one side of more high-ranking males (Schroder, 1973 for chum salmon). However, this hierarchy system is not stable and continuous fights and agonistic displays are performed in order to maintain it.

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* (**Figures 12 & 13**). During *probing* the female rises her caudal fin, flexing it upwards off the bottom, as a result her anal fin remains pressed into the gravel and her full body lays in an angle within the nest depression. She then shakes the fin inside the bottom, possibly using it to test the intergravel depth and condition (**Table 2** for Atlantic salmon). Additionaly, females also use their pelvic and caudal fins to assess nest readiness (Hartman, 1970 for rainbow trout).



Figures 12 -13. Details of a coho salmon female *probing* her nest. Observe in the right picture how the anal fin is pressed deeply into the gravel.

Females perform other behaviours that possibly have the same function of testing nest depth and shape. These include *lying* where the female stays motionless in the nest with the pelvic and pectoral fins extended (**Table 2** for bull trout); *passing-probing* where she swims slowly over the nest rubbing the substrate with her pelvic, anal and caudal fins (**Table 2** for chinook salmon); *flexing* where she keeps her tail flexed laterally to one extreme over the nest (**Table 2** for bull trout, sockeye, coho and pink salmon); *swinging* where she turns one of her sides to the substrate and tests the nest with her pelvic fin (**Table 2** for sockeye salmon); and *winding* where the female continually moves her caudal tail from one side to the other (like in the *flexing* posture) while lying motionless over the nest (**Table 2** for coho and pink salmon). During the probing phase the frequency of digging decreases (Tautz & Groot, 1975) and the female spends more time lying within her nest.

Female probing is a signal for males that oviposition is getting closer. As a result, the frequency of courting and fighting behaviours increases noticeably. The dominant male responds to *probings* with *quiverings* (Legget, 1980 for dolly varden; Berejikian et al., 2000 for chinook salmon; Gaudemar et al., 2000 for Atlantic salmon; personal observations for coho, sockeye, chum and pink salmon). At the same time he guards her from other males. 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 & Groot, 1975 for rainbow trout and chum salmon; Berst et al., 1981 for hybrid charrs; Berejikian et al., 1997 for coho salmon; Gaudemar et al., 2000 for Atlantic salmon) and despite being a fighting behaviour; it possibly acts as a courting one due to constant stimulation of the female's dorsal area. When another male approaches the pair, the dominant male will invariably place his body between the female and the encroaching male all he while maintaining an intimidating posture. 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 (**Figures 14-17**).

There are different types of threatening displays that vary in intensity and significance (**Table 3,** discussed in **Chapters 4 & 5**). In addition, there are species-specific displays and when similar threats are used by different species they may be performed in differently (**Chapter 5**). Sometimes a secondary male will respond to a threatening display with another one. For instance, a typical male-male contest over a nesting female could goes as follows: a satellite or newly arrived male approaches the pair from the back. The dominant male moves towards him by performing a *lateral display* (**Figure 14**). The secondary male adopts a *lateral display* posture and both fish swims parallel to one another for a short period of time. If the action persists the dominant male could either launch a direct attack or perform a *T-display* (**Figure 15**) after what he will attack (or fight back if he is attacked). Conversely, if the newcomer, moves downstream or away from the pair the dominant male will often perform *flanking* (**Figure 16**) and/or *tail displays* (**Figure 17**) to drive him off.

Figures 14 & 15. Sockeye salmon male performing lateral display to another male in his left side (left). A chum salmon male is attacked while performing a T-display (right).

Figures 16 & 17. Brook trout male (foreground) in *flanking display* to a male in dorsal display (left). Brown trout male in tail display to a male in the rear; the most backward fish is the female (right).

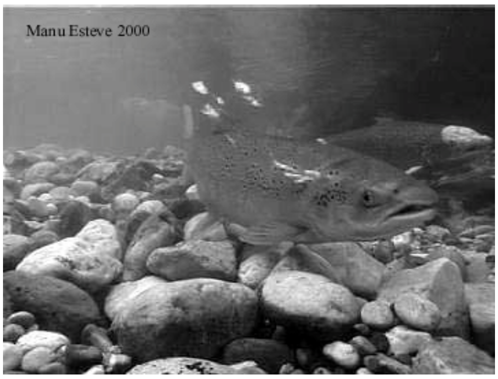
Table 3. Common fighting displays performed by Salmoninae males during the spawning process (the significance of male fighting displays is further discussed on **chapter 4**).

displays	description	possible significance
Frontal display	The head is down and the tail is up. The dorsal fin is depressed (similar to a bottom feeding posture)	Readiness to fight. This posture is often performed by secondary ranking fish ready to fight.
Lateral display	A fish lies in parallel to its opponent with its body flexed upwards and the fins erected.	Dominance exhibition. Normally performed by a dominant male exhibiting the power by making its body vulnerable to an attack.
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.	Dominance exhibition. Extreme demonstration of superiority, the dominant male invites the opponent to an easy attack.
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).	Dominance exhibition. Follows lateral display. It has the function of forcing the opponent to leave.
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.	Dominance exhibition. Follows lateral and/or flanking displays. It has the function of forcing the opponent to leave.

Nest completion and oviposition

As the nest nears completion it gets deeper and consequently the female's body angle during *probing* increases. When this angle reaches approximately 20º the nest is complete (Tautz & Groot, 1975). From this moment oviposition may proceed anytime. However, this gradual increase in the females probing angle is difficult to notice by the human observer. Several other signs, common to all the species (easy to appreciate through underwater video), indicate that oviposition is imminent.

As spawning nears females probe more and dig less. This change in digging and probing frequencies is accompanied by a noticeable increase in a female's respiratory frequency. All female movements in the minutes before oviposition are slower and seem to be performed with less vigor. At this stage, it is common to observe the emission of bubbles through the female's gills (**Figures 18 & 19**). 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 for rainbow trout).

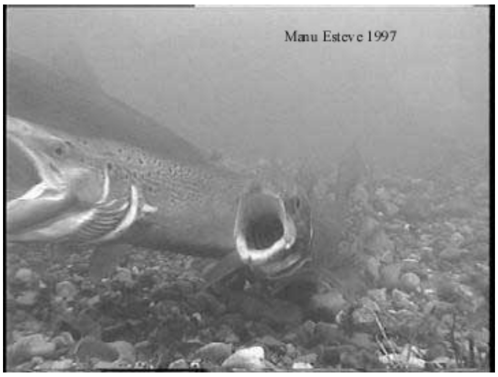


Figures 18 & 19. Atlantic (left) and chinook salmons (right) females emitting bubbles through their gills.

The *probings* immediately before spawning last longer and many times the female will partially gape while performing then (**Figure 20**). Finally, in the immediate seconds before spawning, the female will start *vibrating* her body while *probing* and *gaping*. These three signs are definitive clues for males to synchronize the gamete release (**Figure 21**).

Figure 20 & 21. Pink (left) and chum (right) salmon females gaping during a probing. The chum female has started to vibrate her body indicating to the male on her left that spawning will occur in the immediate future.

However, even after completing all of them, at the last moment the female could decide not to spawn. Instead, she sometimes performs a behaviour known as *false spawning* (**Figures 22 & 23**).



Figures 22 & 23. Atlantic (left) and coho (right) pairs during a false spawning.

A *false spawning* may be considered the last distinctive behaviour before oviposition (discussed in **Chapter 3** below). During it, 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, gaping and vibrating themselves. In some occasions they emit sperm (the sperm cloud can be clearly seen).

During a real 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 24 & 25**). The spreading of pelvic and ventral fins plus gaping possibly helps the pair to remain in a stationary position over the nest (Greeley, 1932). Frequently, males slightly tilt their inferior body in an angle towards the female possibly to better direct the sperm stream towards the eggs. In Atlantic and Pacific salmons the spawning act lasts from 5 to 15 seconds while in brown trout and charr species the act is shorter (personal observations).

Female and male spawning vibration movements differ from 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. In males, this trembling allows to make rapid changes in where the milt is directed and probably helps to ensure fertilization (Satou et al., 1987).

Figures 24 & 25. Chum (left) and sockeye (right) salmon spawning acts.

Real spawning acts are identical to false ones except the female emits a stream of eggs. Eggs are expelled into the deepest part of a nest and are thus difficult to be seen. Consequently, an observer might be in doubt whether a real spawning has occurred. However, after real spawning events females immediately perform a series of rapid and characteristic digs.

When false and real spawning events occur subordinate, as well as sneaker males frequently join the pair to release sperm. This *multiple paternity* phenomenon can occur at the same time the pair is spawning (**Figures 26 & 27**) or immediately afterwards (**Figure 28**). Normally, the time that non-dominate males enter nests aggress with their position in the male dominance hierarchy that surrounded the pair prior to spawning. However, small males following a sneaking tactic are able to release sperm at the same time as the dominant one (personal observations for coho and Atlantic salmon).

Figures 26 & 27. Pink (left) and sockeye (right) *multiple paternity* spawning events.

Figure 28. Two Atlantic salmon males release sperm in the nest some seconds after the female has spawned with the dominant male.

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 & Morrow, 1980 for dolly varden; Johnson, 1991 for arctic charr; Kitano et al., 1994 and personal observations for bull trout). Conversely in the other two genera, females lay only one batch of eggs per nest.

Nest Covering

After releasing their eggs *Oncorhynchus* and *Salmo* females immediately cover them with a rapid series of discrete digs (**Figure 29**). The first few *covering digs* are very gentle and normally do not move any gravel (Tautz & Groot, 1975; personal observations 1-3 tail beats per digging). They have the function of gently locating the released eggs into the interstitial spaces of the nest. As time progresses the occurrence of *covering digs* decreases and they become more intense (personal observations for Pacific and Atlantic salmons).

Figure 29. A Chum salmon female covers her nest by digging.

C*overings 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 (Hartman, 1970 for rainbow trout; Keenleyside & Dupuis, 1988a for pink salmon). In addition, during a *covering dig* females do not curve their bodies as much, instead most of the bending occurs in their caudal peduncles. Within 30 to 40 minutes after spawning eggs are often completely buried, by a depth of gravel equal to the depth of a nest (McCart, 1969 for kokanee and sockeye salmon).

Salvelinus females after spawning perform a unique behaviour consisting in a slow and rhythmic swinging of the body. This is referred to as *undulating* whose apparent function is to disperse recently deposited eggs into the crevices of a nest and possibly to aerate them as well (Needham & Vaughan, 1952 for dolly varden; Fabricius & Gustafson, 1954 for arctic charr; Martin & Olver, 1980 for lake trout; Needham, 1961 and Power, 1980 for brook trout; James & Sexauer, 1997 for bull trout). *Undulating* is a similar but more intense behaviour than *sweeping* described at the nest building stage and again is probably an adaptation of *Salvelinus* to spawning in still waters (Fabricius & Gustafson, 1954). A few minutes (10-20) after ending a series of *spawning acts* charr females decrease the intensity of their *undulating* movements and gradually start to interchange this behaviour with *covering* and nest *building digs* (personal observations for bull trout).

During the nest-covering phase, dominant males move and begin searching for other ripe females. Satellite males, however, would often court a recently spawned female (**Table 2** for Atlantic salmon, Berejikian et al., 1997 for coho). Also, dominant males (when there are no other females available) sometimes remain in the redd attending the spawned female (**Table 2** for chum salmon). This occurs 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 can rest for a period of time or they can 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 for chinook salmon). 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 spawning process (but see **Table 2** for coho and chinook salmon). Whereas, iteroparous females leave their redds for periods during and after nest building.

Table 4. Phases of salmonines spawning behaviour (the change from a phase to the next one is gradual and very often a particular phase would present behaviours from the anterior or next phase).

Phase	Timing	Behaviours		Particularities
		females	males	
(1) nest selection	From the female arrival to the spawning grounds until the firsts 3 subsequent building diggings.	*exploring* *exploratory diggings* *building diggings*	*tastings* *quiverings* *fights* and *displays*	Females in crowded density areas wait in holding places for nesting spaces to become free.
(2) nest building	From the first 3 subsequent building diggings until the first 3 subsequent probings	*building diggings* *weaving* *probings*	*quiverings* *tastings* *fights and displays* *crossovers*	Normally after a digging event females return to their nests by circling. During nest building females travel relatively less than during exploratory diggings. During this stage a dominance hierarchy will be established among the males.
(3) nest probing	From the first 3 subsequent probings until the first false spawning	*probings* *building diggings* *weaving* *resting*	*quiverings* *crossovers* *fights* and *displays*	Respiratory frequency increases. Emission of bubbles occurs. Usually after a digging episode females return to the nest by letting the current to carry them back.
(4) nest completion (oviposition)	From the first false spawning to the real spawning	*Probing, gaping & vibrating* *false spawning* *spawning*	*quivering* *gaping* *spawning*	*Multiple paternity* spawning events are very common.
(5) nest covering	From the real spawning to the total nest covering	*covering diggings* *resting* *defending*	*staying* *leaving the redd*	Covering diggings have fewer tail beats per bout. Iteroparous species do not defend the redd. During diggings females also test the nest covering condition with *probings*

The complete spawning history

A few studies have been able to follow the complete, or partial, spawning history of different salmonines in controlled areas (**Table 5**). This has lead to a better understanding of how the overall spawning process is accomplished in terms of numbers and duration. The main idea coming from these figures is the variation by which females complete the entire spawning process. This idea is key to understanding the importance of *female choice* in the Salmoninae mating system (discussed in **Chapter 4** below).

Table 5. Spawning history of different Salmoninae species.

Ovip. T	n d	n ovips.	Ti	Tn	Species	References	Particularities
3.5 h	250-300	8	3-4 h	_	Atlantic salmon	Jones & King, 1949	The data are from one single female.
_	_	_	4-37 h	3 days	Sea trout	Evans, 1994	Observations were recorded on the wild.
_	_	up to 14	4h-9 days	_	Atlantic salmon	Fleming, 1996	
1h-2 days	_	_	_	5-6 days	Atlantic salmon	Fleming, 1998	
_	_	6-11	9.17 h	4 days	Atlantic salmon	Gaudemar & Beall, 1999	Size-matched pairs were allowed to spawn in absence of competition.
2.7-7.2 h	_	_	_	_	Brook trout	Blanchfield & Ridgway, 1999	Ovip. T. was shorter when females paired with larger males.
_	_	2-6	9.6-16.1 h	_	Chinook salmon	Berejikian et al., 2000	Ti was shorter when females were paired with larger males.
5 h	300-340	_	3 –7 h	_	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 ovips. Number of ovipositions per female.
Ti. Time interval between two ovipositions.
Tn. Total nesting time (does not include the time of redd defense after the last oviposition).