



Phylogeny and Spawning Behaviour

5. Phylogeny and Spawning Behaviour

Introduction

“The behaviour of closely related species is more similar than that of distantly related ones.”
Hinde & Tinbergen (1958, p. 261)

“The more closely related the species are, the more similar they tend to be”
Harvey and Purvis (1991)

These two homologous sentences separated by thirty-three years captured the idea anticipated by Darwin (1859 & 1871), continued by the founders of ethology Charles Whitman and Oskar Heinroth (Whitman, 1899; Heinroth, 1911), and later developed or experimentally demonstrated by (among others) Lorenz Konrad and Niko Tinbergen (Lorenz, 1941b, 1950 & 1958; Tinbergen, 1951, 1952a & 1959). Behaviour, the same as morphology, is inherited. Despite this clarity, a vigorous debate disputing the utility of behaviour in systematics went on during the years separating both sentences (see McLennan et al., 1988 and Brooks & McLennan, 1991 & 2002).

At least three reasons were given to consider behaviour a poor phylogenetic tool. First, behavioural traits are labile (Atz, 1970). Second, they are difficult to measure. Third, contrary to morphology, behaviour does not leave historical records. The first argument implies that behavioural characters are likely to have a high level of homoplasy (similar form due to convergence or reversal) (Kennedy et al., 1996). The second and third arguments express the difficulty of obtaining reliable behavioural data (see Gittleman & Decker, 1994). The three of them together contain the most fundamental problem with behaviour: the difficulty of recognizing homologous traits (Paterson et al., 1995).

Several authors, however, have challenged this view by demonstrating the utility of behaviour in phylogenetic studies (McLennan et al., 1988; Prum, 1990; McLennan, 1991; Wenzel, 1992; de Queiroz & Wimberger, 1993; McLennan, 1993; Kurt & Hartl, 1995; Paterson et al., 1995; Gittleman et al., 1996; Irwin, 1996; Kennedy et al., 1996; Wimberger & de Queiroz, 1996; Kennedy et al., 2000; McLennan & Mattern, 2001).

Using behaviour to discuss or to infer phylogenies is now growing at an accelerated rate, however, there are very few studies related to salmonids. Noakes (1980) compared social

behaviour between and within species in young charrs. Other works have compared life history traits or used them to discuss phylogenies (Hutchings & Morris, 1985; Smith & Stearley, 1989; McDowall, 1997 & 2001; Marshall et al., 1998; Fleming, 1998; Crespi & Teo, 2002). I am only aware of two authors that have mapped different behavioural traits related to reproduction on a tree (morphology-based) to discuss their possible evolution (Stearley, 1992; McLennan, 1994). No studies have used spawning behaviour (or any other type of behaviour) to infer salmonid phylogenies.

I presume that this lack is due to the difficulty of studying, following a homogenous methodology, the behaviour of a group of fish that often spawn under harsh weather conditions or in remote places. This is frustrating since, as suggested by Gittleman & Decker (1994), mating systems, display behaviour and other aspects of reproduction, generally show strong congruence with phylogeny. In addition, by examining and comparing spawning behaviour we can formulate hypotheses explaining the sequence of events that took place in the evolutionary history of this group, which in turn provides fuel to answer theoretical and conservation problems.

Salmoninae Phylogeny

Despite the long history studying salmonid phylogenies, complete agreement among researchers has not yet been reached (**Table 1**). Authors agree on the monophyletic status of the three clades *Salmo*, *Oncorhynchus* and *Salvelinus*. Most of the studies also agree on the placement of some of the species within these clades. For example, among Pacific salmon, two subgroups have been traditionally recognized, one containing coho and chinook, and the other formed by pink, sockeye, and chum (Domanico et al., 1997). Many authors then place cutthroat, steelhead and masu salmon in a third clade basal to the other two groups (Crespi & Fulton, 2004 and references therein).

Differences of opinion, however, appear in one major and two minor points. First, authors disagree on the relative position of the genera. Some studies identify *Salmo* as the basal genus of the clade *Oncorhynchus* plus *Salvelinus*, while others propose *Salvelinus* as the basal genus of the clade *Oncorhynchus* plus *Salmo*. Second, there is disagreement over sister relationships within *Salvelinus* and *Oncorhynchus*. The relative positions of the (sockeye, chum, pink) and (masu, cutthroat, steelhead) clades have not been resolved. The same is true for the charr species, as only the clade formed by arctic charr and Dolly Varden has been commonly recognized (**Table 1**).

Table 1. Salmoninae phylogenetic studies.

references	species	type of data	conclusions
Utter et al., 1973	<i>Oncorhynchus</i>	Allozymes	Pink and sockeye are sister species. Masu, is more related to rainbow trout than to the other species in the genus <i>Oncorhynchus</i>
Cavender, 1980	<i>Salvelinus</i>	Morphology	Arctic charr and dolly varden are sister species.
Behnke, 1984	<i>Salvelinus</i>	Morphology	Arctic charr and dolly varden are sister species. Brook charr and lake charr are basal to the other species.
Smith & Stearley, 1989	<i>Oncorhynchus</i>	Life histories	Pink and chum are sister species.
Shedlock et al., 1992	Salmoninae	mtDNA	Pink and chum are sister species.
Stearley, 1992	<i>Oncorhynchus</i>	Morphology	Pink and sockeye are sister species, coho is basal to chinook. Arctic charr and dolly varden; lake charr and bull trout are sister species.
Stearley & Smith, 1993	<i>Oncorhynchus</i>	Morphology	<i>Salmo</i> and <i>Oncorhynchus</i> are sister taxa, <i>Salvelinus</i> is basal to them
Domanico & Phillips, 1995	<i>Oncorhynchus</i>	mt DNA	Pink and chum are sister species
Domanico et al., 1997	<i>Oncorhynchus</i>	ITS1 and ITS2 of nuclear rDNA	coho and chinook are sister species; pink and chum are sister species
Kitano et al., 1997	<i>Oncorhynchus</i>	mtDNA nDNA	Pink and chum; chinook and coho; and steelhead and cutthroat are sister species
Oohara et al., 1997	<i>Oncorhynchus</i>	mtDNA	Pink and chum; coho and chinook; and steelhead and cutthroat are sister species
Phillips & Oakley, 1997	<i>Salvelinus</i>	ITS (internal transcribed spacers)	<i>Salmo</i> and <i>Oncorhynchus</i> are sister taxa. Arctic charr and dolly varden, and coho and chinook are sister species.
Oakley & Phillips, 1999	Salmoninae	genes for growth hormone 1 and 2	<i>Salmo</i> and <i>Oncorhynchus</i> are not sister taxa. Cutthroat and steelhead; coho and chinook; and pink and chum are sister species
Osinov, 1999	Salmoninae	Allozymes	Dolly varden and arctic charr; coho and chinook; and pink and sockeye are sister species.
Wilson & Li, 1999	Salmonidae	morphology	<i>Salmo</i> and <i>Oncorhynchus</i> ; and <i>Hucho</i> and <i>Salvelinus</i> are sister taxa

If we were to draw a consensus tree based on the references in **Table 1**, it would show a distinct lack of resolution (**Figure 1**).

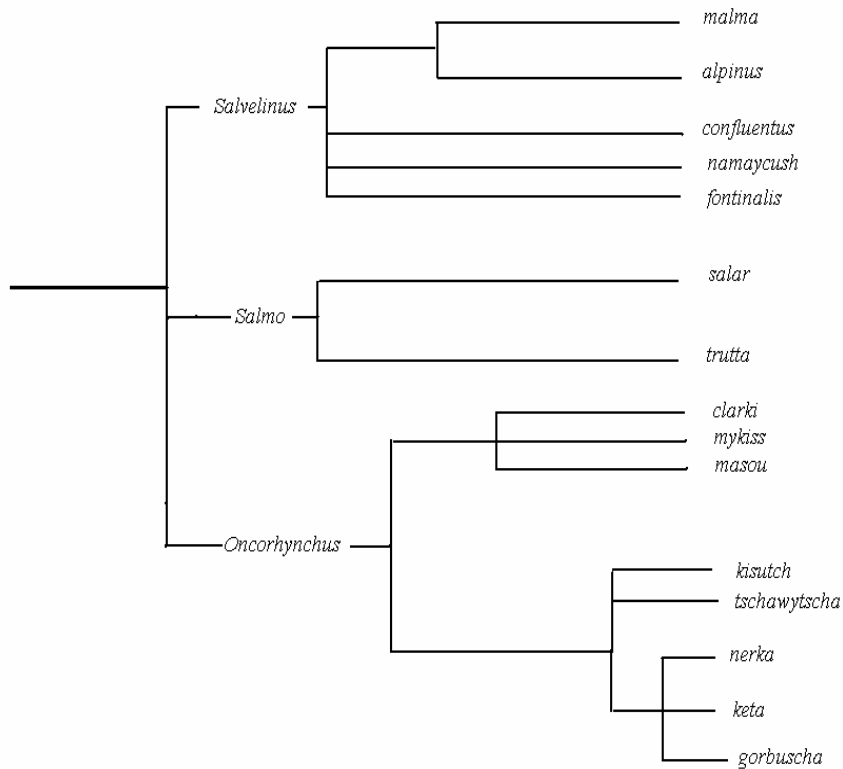


Figure 1. Agreement tree based on references on **Table 1**.

Recently Crespi & Fulton (2004) published a study based on combining all of the existing salmonid molecular data (**Figure 2**). One of the major outcomes of their work is support for the sister relationship between *Salvelinus* and *Oncorhynchus* with *Salmo* basal to them.

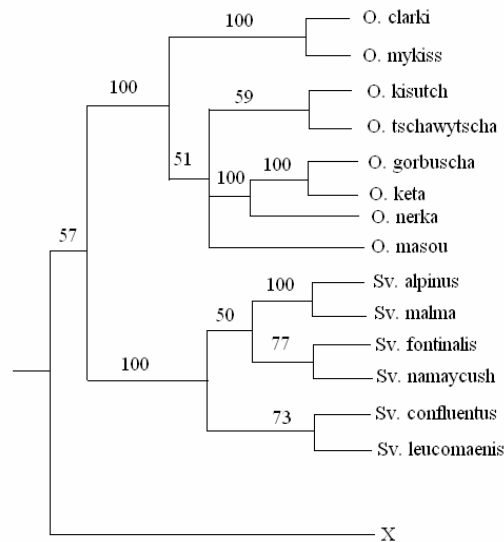


Figure 2. Bootstrap majority-rule based on MP analysis of all nuclear and mitochondrial DNA of Salmonids (redrawn from Crespi & Fulton 2004, only the *Oncorhynchus* and *Salvelinus* species are shown).

In this chapter, first, I will reconstruct the phylogeny of *Oncorhynchus* and *Salvelinus* based only upon behavioural and ecological traits during spawning. In order to do that I assumed that the subfamily positions depicted by Crespi & Fulton (2004) are correct and thus used *Salmo* as the sister group. Second, I will compare my results to our current knowledge of the Salmoninae phylogeny to test the validity of behaviour as a phylogenetic tool. Third, I will discuss the possible evolutionary history of some of the behaviours performed during spawning including predictions for missing characters.

Methods

Forty-four behavioural and ecological traits related to salmonid reproduction were used to infer the *Oncorhynchus* plus *Salvelinus* phylogeny using *Thymallus*, *Hucho* and *Salmo* as outgroups (**Table 2; Figure 3**). Data was primarily collected by underwater video recordings (see **Chapter 2**). Additionally, literature references were used for life history traits and for behavioural ones among the species not observed. The trout of western areas of the Southern USA and Northern Mexico (*O. gilae* and *O. chrysogaster*), as well as the white spotted charr of Eastern Asia (*S. leucomaenis*) were not included because behavioural data were not available (**Chapter 1**).

Table 2. Salmonid species used in this phylogenetic study

Outgroups			Ingroup	
Thymallinae		Salmoninae		
<i>Thymallus</i>	<i>Hucho</i>	<i>Salmo</i>	<i>Salvelinus</i>	<i>Oncorhynchus</i>
Arctic Grayling <i>T. arcticus</i>	Huchen <i>H. hucho</i>	Brown Trout / Sea trout <i>S. trutta</i>	Lake Charr <i>S. namaycush</i>	Cutthroat trout <i>O. clarki</i>
		Atlantic Salmon <i>S. salar</i>	Arctic charr <i>S. alpinus</i>	Steelhead / Rainbow trout <i>O. mykiss</i>
			Dolly Varden <i>S. malma</i>	Masu salmon / yamame <i>O. masou</i>
			Bull charr <i>S. confluentus</i>	Chinook salmon <i>O. tshawytscha</i>
			Brook charr <i>S. fontinalis</i>	Coho salmon <i>O. kisutch</i>
				Sockeye salmon / Kokanee <i>O. nerka</i>
				Chum salmon <i>O. keta</i>
				Pink salmon <i>O. gorbuscha</i>

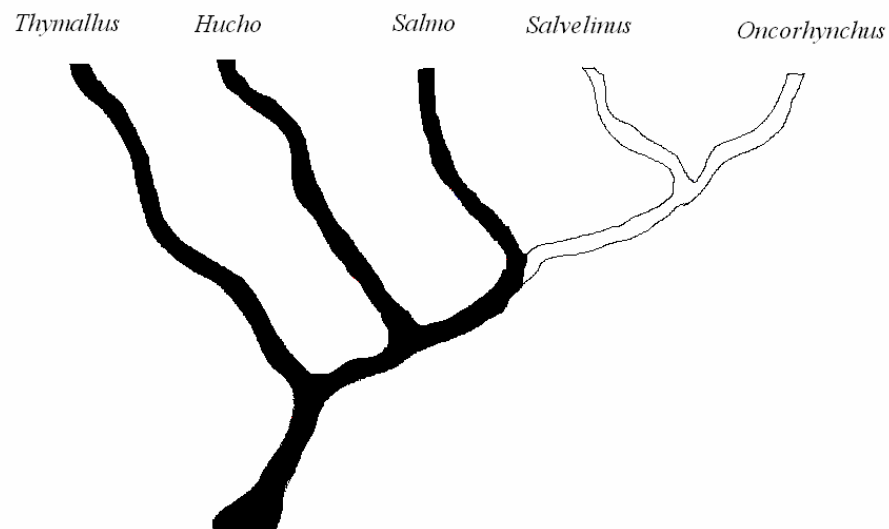


Figure 3. Tree diagram representing the outgroup (black branches) and ingroup (white branches) configuration used in this study.

Phylogenetic analysis

The tree construction methods are based on fundamentals settled by Henning (1950 & 1966) and have been extensively discussed (Maddison et al., 1984; Wiley et al., 1991; Brooks & McLennan, 1991, 1992 & 2002; Mayden & Wiley, 1992). The core concept of phylogenetic analysis is the use of shared derived or apomorphic characters (synapomorphies) to reconstruct common ancestry relationships (Wiley et al., 1991; for a summary of the different methods used to construct phylogenies see Hall, 2001).

The 44 traits were analyzed via maximum parsimony **MP** (employing the outgroup criterion for polarization of characters: Wiley, 1981) using the computer program PAUP 4.0 b10 following the branch and bound searching optional method (Swofford, 2003). The Treeview computer program was employed to visualize and print the inferred trees (Page 1996).

Characters type

Apart from a division into strictly behavioural and ecological or life history traits (discussed below), characters can be divided into three categories:

1. Presence/absence (discrete characters; e.g. female digging 0= yes, 1= no). This category was used most often (36 characters).
2. Differences in performing the same character (discrete characters; e.g. lateral displays 0=upwards; 1= horizontal). Due to intraspecific variation and the difficulty in accumulating enough data, this category was only used when very marked and consistent differences were observed (6 characters).
3. Frequency or duration (continuous characters; e.g. courtship index 0=high; 1=low). This category was used when a statistical test permitted to differentiate at least two states (2 characters). The methods to code these traits are explained below.

All characters were treated as equivalent (unweighted). Character weighting introduces subjectivity into the study because it is based upon the assumption that a particular researcher “knows” which traits are more phylogenetically informative than others (McLennan pers. communication). Although weighting homologies will not affect the analysis, mistakenly giving more weight to homoplasies may produce an incorrect hypothesis of phylogenetic relationships (Brooks & McLennan, 2002).

Of the 44 characters, 35 were binary and 9 multistate. Among the 9 multistate, 5 included a binary plus a “not applicable” condition (see notes on not applicable characters below). All characters were run unordered (see Fitch 1971) because I had no theory-based reason to order the multistate traits a priori.

Autapomorphies (derived character states unique to single taxon), were included in the analysis because they represent evolutionary change even though they are not phylogenetically informative (de Queiroz & Wimberger, 1993). Additionally they can be reevaluated by other scientists as missing data from other species becomes available.

Characters discussion

Some behavioural and life history traits were discussed according the two following protocols:

Individual characters

1. Repeat the analysis taking out the trait subject of discussion.
2. Reconstruct the evolution of the trait in the tree depicted in (1).
3. Discuss the evolution of the trait.
4. Predict the character coding for the missing traits.

Conjunct of characters

1. Map the characters in the tree inferred including all the traits and discuss their evolution.

Predictions of behaviour for the missing traits were done according to the **MP** idea that states that the most likely scenario is the one involving less character changes.

Behavioural versus ecological characters

The division between behavioural and ecological or life history traits is questionable, as any of the second ones results in a definable behaviour. Nevertheless, I have opted to make a distinction and define behavioural traits as those actions that can be witness by an observer from the riverbank (provided he/she has a facility to see the fish underwater). According to this definition all of the behavioural characters of this study can be coded (at least its presence) by an observer looking my underwater video tapes. There are 33 characters of this type (1, 3-8, 10, 11, 13, 16, 18, 19, 21-23, 25-31, 33, 35, 36, 38-44). The remaining 11 characters require knowing the life history of the species and thus have to be based on information collected from the published work.

This definition, however, does not escape some ambiguity; for instance, and observer can witness a single female spawning in different redds (character 20). To resolve these doubts readers should refer to **Table 5**.

List of characters

1. Courtship Intensity Index (CI): CI was defined as the number of quiverings plus diggings per minute a single salmonid pair makes. To calculate it, I have used 1-hour spawning activity samples of spawning pairs from different species. The average number of male quiverings plus female diggings per minute was recorded (**Table 3**). All of the females were in the probing phase (**Table 4 in Chapter 2**). Excepting chum salmon the CI values among species showed a normal distribution (Shapiro-Wilk's W test). A one-way ANOVA test was performed to demonstrate that at least two of the species were different ($F=12.71$; p -value <0.001 ; **Figure 4**). To test for differences between species, CI values for the three outgroup species were grouped together (designated as the "control") and independently compared to the rest of the species. The S-Plus 4.5 statistical software was used to perform comparisons via the Scheffe method (multiple comparisons of independent samples of unequal size to a control; Zar, 1999). The CI's of bull and brook trout were found not to be different from the outgroup one (Scheffe critical point 4.049; $\alpha=0.05$; **Figure 5**).

Table 3. Number of quiverings plus diggings per minute in one-hour samples of spawning activity of different Salmonid pairs (n indicates the number of different nesting females observed).

arctic grayling n=7	brown trout n=9	Atlantic salmon n=5	bull trout n=4	brook trout n=5	steelhead n=6	chinook n=4	coho n=10	sockeye n=11	chum n=10	pink n=5
4.93	6.95	2.71	3.14	1.49	1.43	1.1	0.45	1.52	0.47	0.54
3.65	6.50	1.08	4.82	4.01	1.26	1.00	0.67	0.87	1.08	1
4.15	4.06	1.20	3.33	1.97	2.12	1.50	0.39	0.97	2.08	1.16
3.81	3.86	1.01	2.79	2.14	1.58	1.2	1.63	0.97	3.21	1.19
4.85	3.60	0.60	3.45	2.45	1.77	1.5	1.9	0.97	2.27	1.08
			3.14	1.82	1.77	1.4	0.65	1.28	1.15	2.3
			3.09	1.95		2	0.69	0.75	0.64	1.6
			2.09			1.8	1.27	1.58	0.55	1.83
							0.79	0.82	0.63	
							0.9	0.67	0.71	
							1.49	0.42	1.28	
							1.45	0.35	1.05	
							0.97	0.30	0.98	
								0.37	1.04	
									0.82	
4.28	4.99	1.32	3.23	2.26	1.65	1.44	1.02	0.84	1.20	1.34

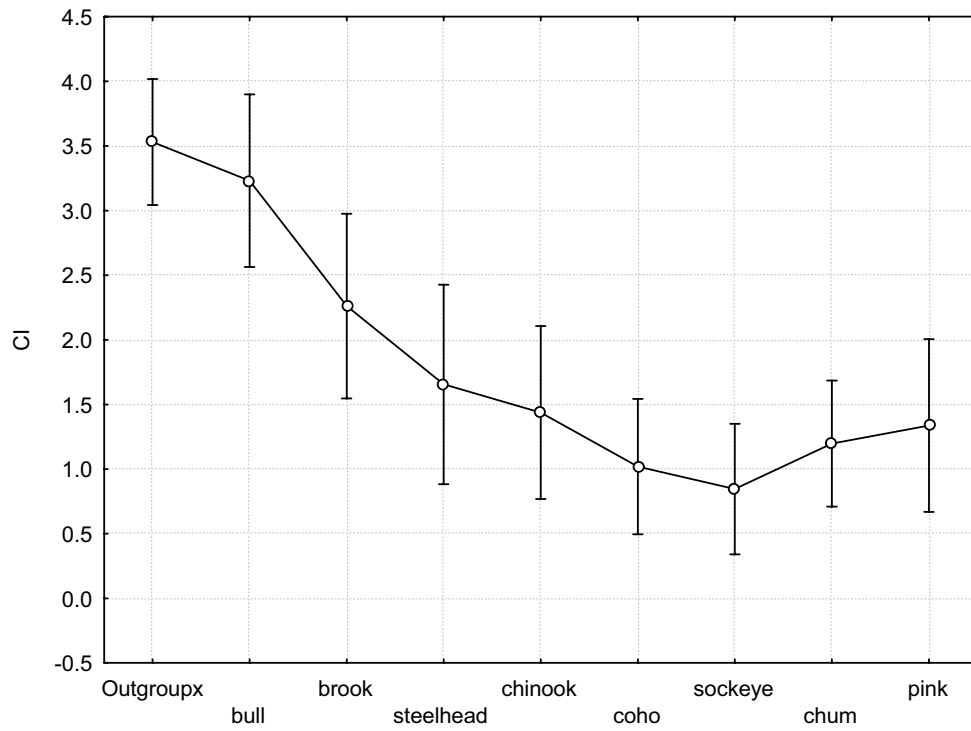


Figure 4. Average number of diggings plus quiverings per minute in one-hour samples of spawning activity of different salmonids mating pairs (vertical bars denote 0.95 confidence intervals).

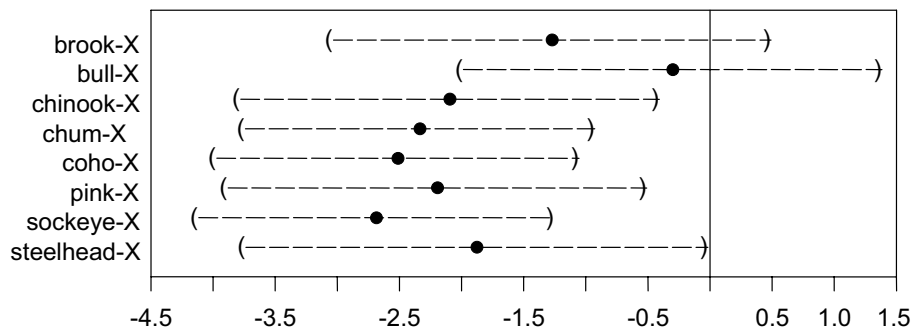


Figure 5. Differences of CI between several salmonine species and the composite outgroup (designed as X; vertical line). Parentheses denote 95 % confidence intervals. Lines crossing the vertical line are similar to the outgroup.

2. Different age classes (dac): Present in species whose members achieve sexual maturation at different ages. This character is autopomorphic for pink salmon.

3. Dilating lower jaw (dlj): During lateral, flanking and tail beat displays, the fish dilates downwards the lower parts of their jaw by erecting the branchiostegal membrane and lowering the hyal bones. As a result, a noticeable protrusion appears in the lower jaw (**Figures 6 & 7**).



Figures 6 & 7. Brown trout dilating the lower jaw

4. Dark spawners (ds): Species were divided into those that continue their spawning activities during dark hours and those that do not. Many species also increase spawning activity during nighttime; however, I did not incorporate that information into this character. I only coded (ds) absent in those species that tend to completely cease their spawning activity during dark hours.

5. Frontal display (fd): The head is down and the tail is up. The dorsal fin is depressed; is similar to a bottom feeding posture (**Figure 8**; see also **Table 3** in **Chapter 2**). The phylogeny of this trait is further discussed below.



Figure 8. Frontal display

6. Female displacement diggings (fdd): Female digging that is not directed towards exploration, nest construction, or burial of eggs (**Figure 9**). It is normally performed in a fighting context. During the displacement digs, females do not bend their bodies as much as in the building diggings (**Chapter 3**). The code 2 was assigned to those species not digging during spawning.



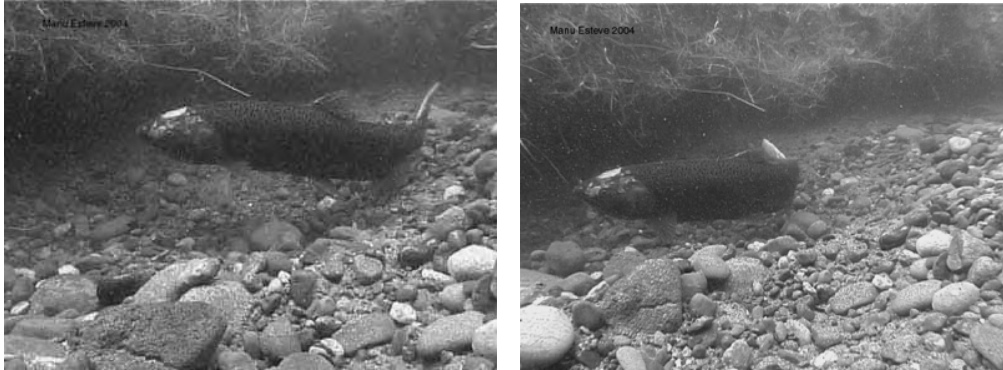
Figure 9. A pink salmon female returns to her nest after an attack and performs a displacement digging.

7. Feeding (feed): Present in species that occasionally feed during the spawning period. During my observations I considered this trait present when species in full nuptial colouration were occasionally seen to feed without ejecting the particle captured. Only in the truly non-feeder species the digestive track has wasted away by the time of spawning (Watson, 1999).

8. Female digging (fem d): Present in species in which females dig gravel depressions with their caudal fin (**Figures 8 & 9** in **Chapter 2**). Within the ingroup, this character is autapomorphic for lake charr.

9. Fry-freshwater (f-fw): Species were divided into those in which the fry always go to sea after emergence from the gravel, those in which the fry only occasionally go to sea and those in which the fry always stay in freshwater for the rearing period.

10. Flexing (flex): Probing behaviour by which the female keeps her tail flexed laterally to one extreme while lying over the nest (**Figures 10 & 11**).



Figures 10 & 11. Coho salmon female performing flexing behaviour

11. Female nest replacement (fnr): Present in species in which female fighting leads to nest replacement by an incoming female. In semelparic species, it is common for females in the late stages of nest defense to be evicted from their nest by new females. I therefore only coded (fnr) present in those species in which the behaviour is common during the nest construction phase (**Table 4 in Chapter 2**).

12. Freshwater populations (fwpop): Present in diadromous species in which it is common to have populations completing the entire life cycle in freshwater (i.e. rainbow trout for *O. mykiss*, kokanee for *O. nerka*, yamame for *O. masou*). I only coded this trait present when freshwater populations were common in the species. Such species frequently have stocks in which entire breeding populations spend their whole lives in freshwater, having no migrations to and from the sea. I did not include species that occasionally have individuals maturing in freshwater (e.g., marginal individuals of coho and sockeye salmon commonly called residuals; see Krogius 1981). Neither did I include species that have evolved a non-migratory life history when transplanted out of their natural habitat (e.g. chinook salmon in New Zealand; pink salmon in the Great Lakes)

13. High snout-lateral displays (hs-ld): Present in species that performs lateral displays in an upward position (with their snout more elevated than their tail). Frequently the fish snout breaks the water surface (**Figure 12; Table 3 in Chapter 2**). The phylogeny of this trait is further discussed below.



Figure 12. Sockeye salmon performing hs-ld.

14. Intertidal spawning (int-s): Present in species with populations that sometimes spawn in intertidal waters. The character was divided into species that often, seldom or never spawn in intertidal waters.

15. Life cycle (lc): Species are divided into those having an entire freshwater cycle; those being amphidromous (amphidromy involves migrations between freshwater and the sea, in both directions, but not for breeding) and those being anadromous (anadromy involves feeding and growth at the sea and reproduction in the rivers). Species that have both anadromous and freshwater populations were considered anadromous. Species that have both anadromous and amphidromous populations were considered amphidromous (e.g. sea trout). The phylogeny of this trait is further discussed below.

16. Lateral displays with arched body (ld-ab): Species were divided into those performing lateral displays with their bodies arched and those performing lateral displays maintaining a horizontal position. The species on which (ld-ab) is present maintain their heads and tail slightly flexed upwards while performing this display (**Figure 13; Table 3 in Chapter 2**). The phylogeny of this trait is further discussed below.



Figure 13. Brook trout male performing (ld-ab).

17. Long ocean migrations (lom): Species were divided into those that perform long migrations in their ocean phase and those that stay in ocean waters close to their rivers' estuary.

18. Male digging (md): Present in species in which males occasionally dig the gravel with their tails. This behaviour is probably a displacement reaction. It is similar to female nest digging but with fewer tail beats per dig (**Figures 8 & 9 in Chapter 3; discussed in Chapter 3**). The phylogeny of this trait is further discussed below.

19. Male-female attack (mfa): Present in species in which males frequently attack newly arriving females.

20. Multiple redd spawners (mrs): Present in species where females sometimes lay eggs in two or more noncontiguous locations.

21. Massive spawnings (ms): Present in species with high spawning densities. I measured this trait according to the minimum number of contiguous nesting females. Whenever I observed 10 or more contiguous nesting females from the riverbank, I coded (ms) to be present. Normally, in these species complete river sections were crowded with spawning fish.

22. Male territoriality (mt): Present in species in which the male establishes a territory and defends it from other males before females arrive and start nest building. In these species, male-male contests are common before females' appearance.

23. Nest absence (na): Present in species in which females frequently abandon their nests for periods of time. I only coded for this behaviour when I repeatedly saw females of a particular species to abandon their nest for periods of over 30 minutes.

24. Over winter at sea (ow): Present in species in which is common to spend, at least, a full winter in the ocean.

25. Precocious maturation (pm): Sexual maturity at the parr stage. The phylogeny of this trait is further discussed below.

26. Post spawning digging (psd): Egg covering behaviour. Present in species in which the female immediately digs the gravel after egg release. All the salmonine females included in the ingroup, except for lake charr, perform diggings after egg release that contributes to egg covering. However, in my personal observations, I only coded for (psd) presence when the female was seen to dig, at least one time, within 15 seconds after spawning. The phylogeny of this trait is further discussed below.

27. Post-spawning nest defense (psnd): Females remain guarding their nests after their last oviposition. In semelparous species, the guarding extends until the female's death.

28. Quivering length (ql): Quivering duration in seconds. I calculated ql as the average quivering duration (0.25 sec. approximations) of approximately 50 quiverings from at least 2 different males for each of the species observed (**Table 4**). No normality test was performed, as data were collected (due to error) without calculating the average of quivering duration per male in each hour of spawning sample (see “polling fallacy”, Martin & Bateson, 1994 pp. 34). However, the high number of recorded observations (495 quiverings in 79 different males) plus the mean and medians distributions presumed a normal distribution (**Figure 14**). A one-way ANOVA test was performed to demonstrate that at least two of the species were different ($F= 15.05$; $p\text{-value} < 0.001$; **Figure 14**). To test for differences between species, ql values for the three outgroup species were grouped together (designated as the “control”) and independently compared to the rest of the species. The S-Plus 4.5 statistical software was used to perform comparisons via the Scheffe method (multiple comparisons of independent samples of unequal size to a control; Zar, 1999). The ql values of Dolly Varden and brook trout were found to be different from the outgroup one (Scheffe critical point 4.1343; $\alpha=0.05$; **Figure 15**). (Taking this trait out of the analysis does not change the final tree configuration).

Table 4. Quiverings average duration and type in different salmonines (n is the number of quiverings measured, N is the number of males observed).

Species	n	N	average duration (seconds)	amplitude	frequency	Type
grayling	40	5	2.20	high	low	I
brown trout	40	9	1.46	high	low	I
Atl. salmon	40	5	1.94	high	low	I
dolly varden	19	2	1.02	low	high	II
bull trout	50	4	1.70	low	high	II
brook trout	33	7	0.74	low	high	II
steelhead	50	7	1.72	high	low	I
chinook	23	3	1.67	high	low	I
coho	50	9	1.63	high	low	I
sockeye	50	11	1.59	low	high	II
chum	50	10	1.49	high	low	I
pink	50	7	1.72	high	low	I

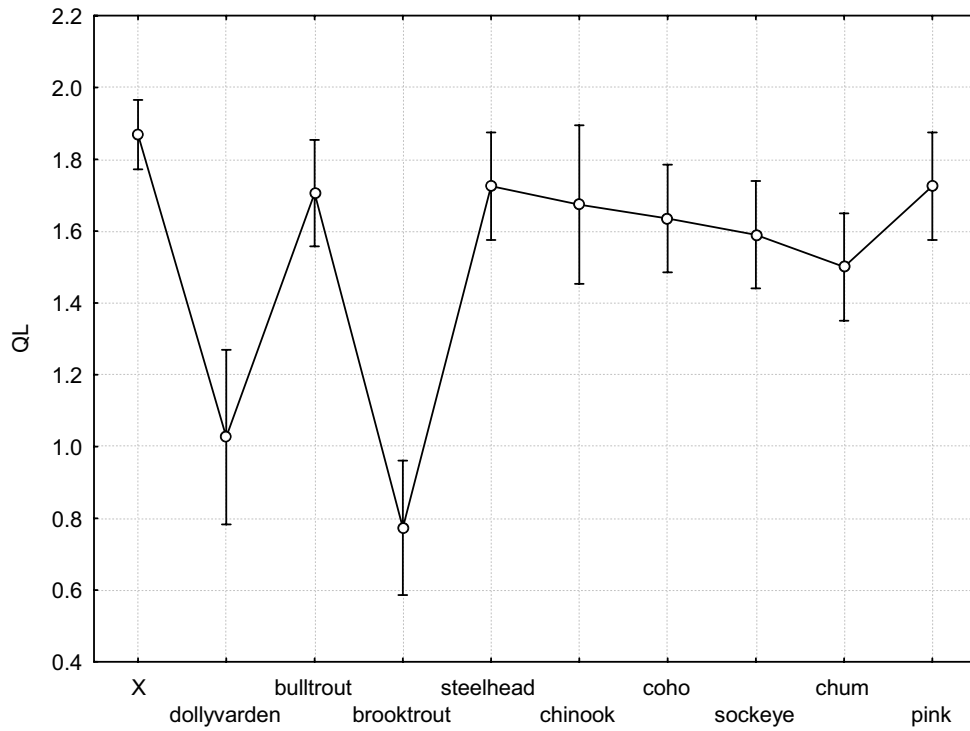


Figure 14. Average duration of quiverings per species (vertical bars denote 0.95 confidence intervals).

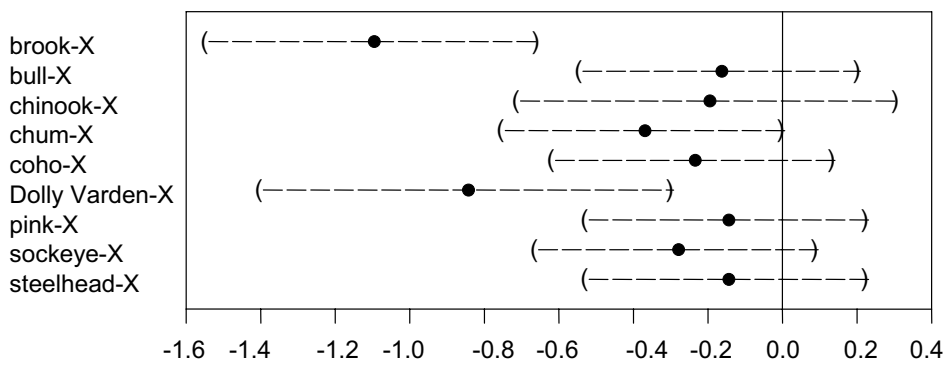


Figure 15. Differences of ql between several salmonine species and the composite outgroup (designed as X; vertical line). Parentheses denote 95 % confidence intervals. Lines crossing the vertical line are similar to the outgroup.

29. Quivering type (qt): Species were divided into those performing high amplitude and low frequency quiverings (type I) and those performing low amplitude and high frequency quiverings (type II). As the cameras I used (25 frames/sec) did not allow me to measure exact amplitudes or frequencies I used my naked eye to divide the species into both types. To test for the validity of this method I repeated the process with two anonymous viewers and obtained 100% agreement. The phylogeny of this trait is further discussed below.

30. Redd absence during hours of high sun (ra-hs): Species were divided into those that use to interrupt their spawning activity in midday hours in clear days, and those that do not.

31. Sequential covering diggings (scd): Present in species in which females cover their nest after each egg deposition. The phylogeny of this trait is further discussed below.

32. Semelparity (semel): One unique reproductive event in the life. It is opposed to iteroparity. The phylogeny of this trait is further discussed below.

33. Spawning moving forward (sp-mfw): Present in species in where during the spawning act both male and female slowly move forward.

34. Spawning habitat (sph): Species were divided into those that predominantly spawn in streams, those that preferentially use streams but frequently spawn in lakes and those that preferentially use lakes but frequently or occasionally use streams.

35. Series of quiverings (sq): Continuous quiverings separated by a few seconds (1-3). Normally the male alternates female sides while performing this behaviour. I only coded for this behaviour when I saw a minimum of three quiverings in 10 seconds.

36. Sequential spawning (ssp): Present in species in which the spawning act is performed in sequences separated by some seconds or a few minutes (more than one batch of eggs per nest pocket). The phylogeny of this trait is further discussed below.

37. Spawning time of the year (st): Distinguishes species spawning during the spring from those spawning in the fall.

38. Tail bending (tb): The female, during building digs, starts bending her tail prior to her body. I used frame-by-frame analysis to distinguish this trait (1 sec= 25 frames).

39. Tail beat display-downwards (tbd –dw): Present in species in which the tail beat display (Table 3 in Chapter 2) is frequently performed with a downward inclination. The head lies in a downward position respect to the tail.

40. T-display (T-d): Perpendicular body presentations in a fighting context (Figure 16; Table 3 in Chapter 2; the significance of this trait is discussed in Chapter 4). Perpendicular positions during rivalry fighting are common in all the salmonines (pers. observations). I therefore only coded (T-d) present when the display position was maintained for a minimum of 2 seconds. The phylogeny of this trait is further discussed below.



Figure 16. T display in pink salmon

41. Undulating before spawning (und1): Nest cleaning movement. The female cleans the gravel by performing undulating movements. During this movement the tail is not flexed upwards but remains horizontal very often touching the gravel. This is the same behaviour called sweeping by Fabricius & Gustafson (1954) (Chapter 2).

42. Undulating after spawning (und2): Egg covering movement. Present in species in which the female performs a series of undulating movements after spawning to distribute her eggs into the gravel interstices. Normally females perform this behaviour above the substrate without physically touching the gravel.

43. Violent quiverings (violq): Male quivering behaviour consisting of violent shakings. When compared with normal quiverings (**violq**) have a lower frequency, but higher amplitude (i.e., stronger shaking; **Figure 17**). In addition (**violq**) last longer than normal quiverings and are normally performed away from the female. This behaviour was called *trembling* by other authors (Armstrong & Morrow, 1980) and is most probably a displacement reaction. The phylogeny of this trait is further discussed below.



Figure 17. A bull trout male violently shakes his body while the female digs the nest.

44. Winding-probing (wind): Probing movement. The female moves her caudal tail laterally from one side to the other in the probing position and shakes her anal fin inside the gravel.

Table 5. List of characters used on this study. Life history traits are marked with *.

	Characters	category	coding
1	Courtship Index (CI)	behaviour	binary
2*	Different age classes (dac)	life history	binary
3	Dilating lower jaw (dlj)	behaviour	binary
4	Dark spawners (ds)	behaviour	binary
5	Frontal display (fd):	behaviour	binary
6	Female displacement diggings (fdd)	behaviour	multistate
7	Feeding (feed)	behaviour	binary
8	Female digging (fem d)	behaviour	multistate
9*	Fry-freshwater (f-fw)	life history	multistate
10	Flexing (flex)	behaviour	binary
11	Female nest replacement (fnr)	behaviour	binary
12*	Freshwater populations (fwpop)	life history	multistate
13	High snout-lateral displays (hs-ld)	behaviour	binary
14*	Intertidal spawning (int-s)	life history	multistate
15*	Life cycle (lc)	life history	multistate
16	Lateral displays with arched body (ld-ab)	behaviour	binary
17*	Long ocean migrations (lom)	life history	binary
18	Male digging (md)	behaviour	binary
19	Male female attacks (mfa)	behaviour	binary
20*	Multiple redd spawners (mrs)	life history	binary
21	Massive spawnings (ms)	behaviour	binary
22	Male territoriality (mt)	behaviour	binary
23	Nest absence (na)	behaviour	binary
24*	Over winter at sea (ow)	life history	binary
25	Precocious maturation (pm)	behaviour	binary
26	Post spawning digging (psd)	behaviour	binary
27	Post-spawning nest defense (psnd)	behaviour	binary
28	Quivering length (ql)	behaviour	binary
29	Quivering type (qt)	behaviour	binary
30	Redd absence during hours of high sun (ra-hs)	behaviour	binary
31	Sequential covering diggings (scd)	behaviour	multistate
32*	Semelparity (semel)	life history	binary
33	Spawning moving forward (sp-mfw)	behaviour	binary
34*	Spawning habitat (sph)	life history	multistate
35	Series of quiverings (sq)	behaviour	binary
36	Sequential spawning (ssp)	behaviour	binary
37*	Spawning time of the year (st)	life history	binary
38	Tail bending (tb)	behaviour	multistate
39	Tail beat display-downwards (tbd -dw)	behaviour	binary
40	T-display (T-d)	behaviour	binary
41	Undulating before spawning (und1)	behaviour	binary
42	Undulating after spawning (und2)	behaviour	binary
43	Violent quiverings (violq)	behaviour	binary
44	Winding-probing (wind)	behaviour	binary

References for character state

The references for each character were based on personal observations and on literature (Tables 6-20). For ecological traits, literature references were favoured and for behavioural traits, personal observations were favoured (provided there were no conflicts with the literature). Character coding was conservative; when I did not have enough data to make a decision, I used the (?) code. Whenever I repetitively observed a particular behaviour, I coded for its presence. However, if I did not observe a behaviour I only coded for its absence when I had enough hours of observation on different individuals to be sure that the behaviour was really “absent”. I only used personal communications from experts in the particular area.

There is a tremendous variation within and between species in the life histories of salmonines (see Wilson 1997). Because of this, some of the characters states refer to the tendency most members of a particular species will follow. For instance, lake charr and Arctic grayling occasionally enter brackish waters, however this is rare and sufficient information exists to code both species as having an entire freshwater cycle. Another example is spawning time of the year, which, although it shows some variability within species, has traditionally been divided into only spring or fall spawners (Watson 1999). Nevertheless, whenever a trait of a polytypic species was too ambiguous to differentiate it into present or absent, I entered a third state to indicate the frequency of occurrence (e.g. intertidal spawning 0 never, 1 seldom, 2 often).

Note on “not applicable” characters

PAUP treats “not applicable” characters the same as missing data (?). This makes the analysis (unnecessarily) ambiguous because the program looks for the best tree treating both codes as the same, which clearly they are not. For example, treating a “not applicable” trait the same as a “missing” trait implies that researchers may someday discover that trait in the species. To overcome this problem it is better to assign a third code to the “not applicable” characters (Brooks & McLennan pers. communication).

For instance, all characters referring to female building digs are “not applicable” for lake charr because female digging is autapomorphically absent in that species. Instead of coding these traits as “not applicable”, I scored lake charr with a 2 for all female digging traits; defining 2 as: females does not dig nest.

Table 6. References for characters 1-3.

	(1) CI 0=high	(2) dac 0=yes	(3) dlj 0=yes
arctic grayling	0 pers. observations (see note 1)	0 Wilson, 1997	0 pers. observations
huchen	?	0 Holcik et al., 1988	?
brown trout	0 pers. observations	0 pers. observations	0 pers. observations
Atlantic salmon	1 pers. observations	0 pers. observations	1 pers. observations
lake charr	?	0 Martin & Olver, 1980	?
arctic char	?	0 Watson, 1999	1 Fabricius, 1953 (see note2)
dolly varden	?	0 pers. observations	?
bull trout	0 pers. observations	0 pers. observations	1 pers. observations
brook trout	0 pers. observations	0 pers. observations	0 pers. observations
cutthroat	?	0 Groot, 1996	?
steelhead	0 pers. observations	0 pers. observations	1 pers. observations
masu	?	0 Groot, 1996	?
chinook	1 pers. observations	0 pers. observations	1 pers. observations
coho	1 pers. observations	0 pers. observations	1 pers. observations
sockeye	1 pers. observations	0 pers. observations	1 pers. observations
chum	1 pers. observations	0 pers. observations	1 pers. observations
pink	1 pers. observations	1 Watson, 1999 (see note 3)	1 pers. observations

Notes

1. As graylings do not perform nest diggings, only quiverings were used to calculate **CI**.
2. Fabricius (1953) reported that **dlj** only occurred in young individuals but not in mature adults, I observed the same in Atlantic salmon.
3. 1-year old and 3-year-old pinks occur occasionally in natural populations (Wilson, 1997).

Table 7. References for characters 4-6.

	(4) ds	0=yes	(5) fd	0=yes	(6) fdd	0=no
arc. grayling	1	pers. observations	0	pers. observations	2	no digging behaviour
huchen	1	Holcik et al., 1988	?		?	
brown trout	0	pers. observations	0	pers. observations	1	pers. observations
Atlantic salmon	0	pers. observations	0	Fleming, 1996	0	pers. observations
lake charr	0	Gunn, 1995 (see note1)	?		2	no digging behaviour
arctic char	1	Fabricius & Gustafson, 1954	0	Fabricius, 1953	?	
dolly varden	1	Groot, 1996	0	pers. observations	?	
bull trout	0	pers. observations	0	pers. observations	0	pers. observations
brook trout	1	pers. observations	0	pers. observations	0	pers. observations
cutthroat	0	Smith, 1941	0	Butler, 1991	?	
steelhead	0	pers. observations	0	Butler, 1991	0	pers. observations
masu	0	Groot, 1996	?		?	
chinook	0	pers. observations	1	S. Schroder pers. com.	1	S. Schroder pers. com.
coho	0	pers. observations	1	pers. observations	1	pers. observations
sockeye	0	pers. observations	1	pers. observations	1	pers. observations
chum	0	pers. observations	1	pers. observations	1	pers. observations
pink	0	pers. observations	1	pers. observations	1	pers. observations

1. Lake charr spawns exclusively at night (Gunn 1995).

Table 8. References for characters 7-9.

	(7) feed	0=yes	(8) fem d	0=yes	(9) f-fw	0=never; 1=sometimes; 2=always
arc. grayling	?		1	pers. observations	0	entire freshwater cycle
huchen	0	Holcik et al., 1988	0	Holcik et al., 1988	0	entire freshwater cycle
brown trout	0	pers. observations	0	pers. observations	0	Groot, 1996
Atl. salmon	0	pers. observations	0	pers. observations	0	Groot, 1996
lake charr	0	Martin & Olver, 1980	1	Gunn, 1995	0	entire freshwater cycle
arctic char	0	Fabricius, 1953	0	Fabricius, 1953	0	Groot, 1996
dolly varden	0	pers. observations	0	pers. observations	0	Armstrong & Morrow, 1980
bull trout	0	pers. observations	0	pers. observations	0	Groot, 1996
brook trout	0	Blanchfield & Ridgway, 1999	0	pers. observations	0	Groot, 1996
cutthroat	0	pers. observations	0	pers. observations	0	Groot, 1996
steelhead	0	Watson, 1999	0	pers. observations	0	Stearley, 1992
masu	0	Watson, 1999	0	Groot, 1996	0	Kato, 1991
chinook	1	Watson, 1999	0	pers. observations	1	Wilson, 1997
coho	1	Watson, 1999	0	pers. observations	1	Wilson, 1997
sockeye	1	Watson, 1999	0	pers. observations	1	Wilson, 1997
chum	1	Watson, 1999	0	pers. observations	2	Kinnison & Hendry, 2004
pink	1	Watson, 1999	0	pers. observations	2	Kinnison & Hendry, 2004

Table 9. References for characters 10-12.

	(10) flex	0=no	(11) fnr	0=yes	(12) fwpop	0=yes
arctic grayling	0	pers. observations	2	no nest building	0	all freshwater
huchen	?		?		0	all freshwater
brown trout	0	pers. observations	0	pers. observations	0	Watson, 1999
Atlantic salmon	0	pers. observations	0	pers. observations	0	Ricker, 1972
lake charr	?		2	no nest building	0	all freshwater
arctic char	?		0	Fabricius, 1953	0	Watson, 1999
dolly varden	?		?		0	Watson, 1999
bull trout	1	pers. observations	?		0	Watson, 1999
brook trout	0	pers. observations	?		0	Watson, 1999
cutthroat	?		0	Smith, 1941	0	Watson, 1999
steelhead	1	pers. observations	?		0	Watson, 1999
masu	?		?		0	Groot, 1996
chinook	?		0	S. Schroder pers. com.	1	Watson, 1999
coho	1	pers. observations	0	pers. observations	1	Watson, 1999
sockeye	1	pers. observations	1	pers. observations	0	Watson, 1999
chum	1	pers. observations	1	pers. observations	1	Watson, 1999
pink	1	pers. observations	1	pers. observations	1	Watson, 1999

Table 10. References for characters 13-15.

	(13) hs-ld	0=no	(14) int-s	0=never; 1=seldom; 2=often	(15) lc	0=fresh. 1= amph. 2=anad.
arctic grayling	0	pers. observations	0	Freshwater	0	Stearley, 1992
huchen	?		0	Freshwater	0	Holcik, 1982
brown trout	0	pers. observations	0	no reports in literature	1	Stearley, 1992
Atl. salmon	0	pers. observations	0	Mills, 1989	2	McLennan, 1994
lake charr	?		0	Freshwater	0	McLennan, 1994
arctic char	?		0	no reports in literature	1	Stearley, 1992
dolly varden	0	pers. observations	0	no reports in literature	1	Stearley, 1992
bull trout	0	pers. observations	0	no reports in literature	1	Stearley, 1992
brook trout	0	pers. observations	0	no reports in literature	1	Stearley, 1992
cutthroat	0	pers. observations	0	Watson, 1999	1	Stearley, 1992
steelhead	0	pers. observations	0	Watson, 1999	1	Burgner et al., 1992
masu	?		0	Watson, 1999	2	Stearley, 1992
chinook	0	pers. observations	1	Wilson, 1997	2	McLennan, 1994
coho	0	pers. observations	0	Watson, 1997	2	McLennan, 1994
sockeye	1	pers. observations	0	Watson, 1999	2	McLennan, 1994
chum	0	pers. observations	2	pers. observations	2	McLennan, 1994
pink	1	pers. observations	2	Heard, 1991	2	McLennan, 1994

Table 11. References for characters 16-18.

	(16) ld-ab	0=no	(17) lom	0=no	(18) md	0=no
arctic grayling	0	pers. observations	0	freshwater	0	pers. observations
huchen	?		0	freshwater	1	Holcik et al., 1988
brown trout	1	pers. observations	0	Watson, 1999	0	pers. observations
Atlantic salmon	0	pers. observations	1	Watson, 1999	0	pers. observations
lake charr	?		0	freshwater	0	Gunn, 1995
arctic char	1	Groot, 1996	0	Watson, 1999	0	Fabricius, 1953
dolly varden	1	pers. observations	0	Watson, 1999	0	no literature reports
bull trout	1	pers. observations	0	Watson, 1999	0	pers. observations
brook trout	1	pers. observations	0	Watson, 1999	0	pers. observations
cutthroat	?		0	Watson, 1999	?	
steelhead	0	pers. observations	1	Watson, 1999	1	B. Berejikian pers. com
masu	?		0	Watson, 1999	?	
chinook	0	pers. observations	1	Healey, 1991	1	B. Berejikian pers. com
coho	0	pers. observations	1	Sandercock, 1991	1	Healey & Prince, 1998
sockeye	0	pers. observations	1	Burgner, 1991	1	pers. observations
chum	0	pers. observations	1	Salo, 1991	1	pers. observations
pink	0	pers. observations	1	Heard, 1991	1	pers. observations

Table 12. References for characters 19-21.

	(19) mfa	0=yes	(20) mrs	0=yes	(21) ms	0=no
arctic grayling	0	pers. observations	0	pers. observations	0	pers. observations
huchen	?		0	Fukushima, 1994	0	no literature reports
brown trout	0	pers. observations	0	pers. observations	0	pers. observations
Atlantic salmon	1	pers. observations	0	Gaudemar et al., 2000	0	pers. observations
lake charr	?		0	Watson, 1999	0	no literature reports
arctic char	0	Fabricius, 1953	0	Fabricius, 1953	0	no literature reports
dolly varden	0	Watson, 1999	0	Watson, 1999	0	no literature reports
bull trout	0	pers. observations	0	Watson, 1999	0	pers. observations
brook trout	0	pers. observations	0	pers. observations	0	pers. observations
cutthroat	1	Watson, 1999	0	Smith, 1941	0	pers. observations
steelhead	1	Watson, 1999	0	Watson, 1999	0	pers. observations
masu	1	Watson, 1999	0	Y. Koseki pers. com.	0	Yamamoto & Edo, 2002
chinook	1	Watson, 1999	0	Bentzen et al., 2001	0	pers. observations
coho	1	Watson, 1999	0	pers. observations	0	pers. observations
sockeye	1	Watson, 1999	1	Watson, 1999	1	pers. observations
chum	1	Watson, 1999	1	Watson, 1999	1	pers. observations
pink	1	Watson, 1999	1	Watson, 1999	1	pers. observations

Table 13. References for characters 22-24.

	(22) mt 0=yes	(23) na 0=yes	(24) ow 0=no
arctic grayling	0 Watson, 1999	0 no nesting behaviour	0 freshwater
huchen	0 Stearley, 1992	0 Holcik et al., 1988	0 freshwater
brown trout	0 pers. observations	0 pers. observations	0 Stearley, 1992
Atlantic salmon	1 pers. observations	0 pers. observations	1 Watson, 1999
lake charr	1 Wilson, 1997	0 no nesting behaviour	0 Freshwater
arctic char	0 Fabricius, 1953	?	0 Watson, 1999
dolly varden	0 Legget, 1980	0 James & Sexauer, 1997	0 Watson, 1999
bull trout	0 Watson, 1999	0 pers. observations	0 Watson, 1999
brook trout	0 pers. observations	0 pers. observations	0 Watson, 1999
cutthroat	1 Watson, 1999	0 Cramer, 1940	0 Stearley, 1992
steelhead	1 Watson, 1999	0 pers. observations	1 Stearley, 1992
masu	1 Watson, 1999	0 Y. Koseki pers. com.	1 Stearley, 1992
chinook	1 Watson, 1999	0 pers. observations	1 Stearley, 1992
coho	1 Watson, 1999	0 pers. observations	1 Stearley, 1992
sockeye	1 Watson, 1999	1 pers. observations	1 Stearley, 1992
chum	1 Watson, 1999	1 pers. observations	1 Stearley, 1992
pink	1 Watson, 1999	1 pers. observations	1 Stearley, 1992

Table 14. References for characters 25-27.

	(25) pm 0=yes	(26) psd 0=yes	(27) psnd 0=no
arctic grayling	1 Haugen & Rygg, 1996	2 no digging behaviour	0 pers. observations (see note 1)
huchen	1 Holcik et al., 1988	1 Holcik et al., 1988	0 Holcik et al., 1988
brown trout	0 Evans, 1994	0 pers. observations	0 Fleming, 1998
Atlantic salmon	0 Fleming, 1996	0 pers. observations	0 Fleming, 1998
lake charr	1 Fleming, 1998	2 no digging behaviour	0 no literature reports
arctic char	0 Jonsson & Jonsson, 2001	1 Fabricius, 1953	0 Fleming, 1998
dolly varden	0 Maekawa & Hino, 1986	1 pers. observations	0 Fleming, 1998
bull trout	0 James & Sexauer, 1997	1 pers. observations	0 Fleming, 1998
brook trout	0 Blanchfield & Ridgway, 1999	1 Needham, 1961	0 Fleming, 1998
cutthroat	0 Fleming, 1998	0 Smith, 1941	0 Groot, 1996
steelhead	0 Needham & Tautz, 1934	0 pers. observations	0 Fleming, 1998
masu	0 Tsiger et al., 1994	0 Groot, 1996	1 Kato, 1991
chinook	0 Taylor, 1989	0 pers. observations	1 Fleming, 1998
coho	1 no reports in the literature	0 pers. observations	1 Fleming, 1998
sockeye	1 no reports in the literature	0 pers. observations	1 Burgner, 1991
chum	1 no reports in the literature	0 pers. observations	1 Schroder, 1981
pink	1 no reports in the literature	0 pers. observations	1 Heard, 1991

Notes

1. Grayling females do not build nests, so I coded the species with a 0 because females don't guard the location where they laid their eggs.

Table 15. References for characters 28-30.

	(28) ql 0 long	(29) q type 0=type I; 1=type II	(30) ra-hs 0=yes
arctic grayling	0 pers. observations	0 pers. observations	1 pers. observations
huchen	?	?	?
brown trout	0 pers. observations	0 pers. observations	0 pers. observations
Atlantic salmon	0 pers. observations	0 pers. observations	0 pers. observations
lake charr	?	?	0 night spawners
arctic char	?	?	?
dolly varden	1 pers. observations	1 pers. observations	1 pers. observations
bull trout	0 pers. observations	1 pers. observations	0 pers. observations
brook trout	1 pers. observations	1 pers. observations	1 pers. observations
cutthroat	?	?	?
steelhead	0 pers. observations	0 pers. observations	0 pers. observations
masu	?	?	?
chinook	0 pers. observations	0 pers. observations	0 pers. observations
coho	0 pers. observations	0 pers. observations	0 pers. observations
sockeye	0 pers. observations	1 pers. observations	1 pers. observations
chum	0 pers. observations	0 pers. observations	1 pers. observations
pink	0 pers. observations	0 pers. observations	1 pers. observations

Type I: high amplitude and low frequency. Type II: low amplitude high frequency

Table 16. References for characters 31-33.

	(31) scd 0=yes	(32) semel 0=no	(33) sp-mfw 0=no
arctic grayling	2 no digging	0 Stearley, 1992	0 pers. observations
huchen	1 Holcik et al. 1988	0 Fleming, 1998	1 Holcik et al., 1988
brown trout	0 pers. observations	0 Fleming, 1998	0 pers. observations
Atlantic salmon	0 pers. observations	0 Fleming, 1998	0 pers. observations
lake charr	2 no digging	0 Fleming, 1998	?
arctic char	1 Fabricius, 1953	0 Fleming, 1998	1 Fabricius & Gustafson, 1954
dolly varden	1 pers. observation	0 Fleming, 1998	0 pers. observations
bull trout	1 pers. observation	0 Stearns & Hendry, 2004	0 pers. observations
brook trout	0 Needham, 1961	0 Fleming, 1998	?
cutthroat	0 Smith, 1941	0 Fleming, 1998	0 Smith, 1941
steelhead	0 pers. observation	0 Fleming, 1998	0 pers. observations
masu	0 Kato 1991	1 Crespi & Fulton, 2004 (see note 1)	?
chinook	0 pers. observation	1 Fleming, 1998 (see note 2)	0 pers. observations
coho	0 pers. observation	1 Fleming, 1998	0 pers. observations
sockeye	0 pers. observations	1 Fleming, 1998	0 pers. observations
chum	0 pers. observation	1 Fleming, 1998	0 pers. observations
pink	0 pers. observation	1 Fleming, 1998	0 pers. observations

Notes

1. Mature male parr may survive to breed again (Tsiger et al., 1994); additionally the freshwater form of masu, named yamame may spawn two or more times (Groot, 1996).
2. Some precocious males have been reported to survive (Healey, 1991)

Table 17. References for characters 34-36.

	(34) sph 0=streams	(35) sq 0=yes	(36) ssp 0=no
arctic grayling	0 Watson, 1999	0 pers. observations	0 pers. observations
huchen	0 Watson, 1999	?	1 Holcik et al., 1988
brown trout	1 Watson, 1999	0 pers. observations	0 Groot, 1996
Atlantic salmon	0 Watson, 1999	0 pers. observations	0 pers. observations
lake charr	2 Wilson, 1997	?	1 Martin & Olver, 1980
arctic char	2 Wilson, 1997	?	1 Johnson, 1991
dolly varden	0 Wilson, 1997	0 pers. observations	1 Legget, 1980
bull trout	0 Wilson, 1997	0 pers. observations	1 Kitano et al., 1994
brook trout	0 Wilson, 1997	0 pers. observations	0 Needham, 1961
cutthroat	1 Wilson, 1997	?	0 Smith, 1941
steelhead	1 Wilson, 1997	0 pers. observations	0 Needham & Taft, 1934
masu	0 Watson, 1999	?	0 Kato, 1991
chinook	0 Wilson, 1997	1 pers. observations	0 pers. observations
coho	0 Wilson, 1997	0 pers. observations	0 pers. observations
sockeye	1 Wilson, 1997	1 pers. observations	0 pers. observations
chum	0 Wilson, 1997	1 pers. observations	0 pers. observations
pink	0 Wilson, 1997	1 pers. observations	0 pers. observations

Table 18. References for characters 37-39.

	(37) st 0=fall	(38) tb 0=yes	(39) tbd-dw 0=yes
arctic grayling	1 Fabricius, 1955	2 no digging behaviour	1 pers. observations
huchen	1 Holcik et al., 1988	?	?
brown trout	0 Groot, 1996	0 pers. observations	0 pers. observations
Atlantic salmon	0 Groot, 1996	0 pers. observations	0 pers. observations
lake charr	0 Groot, 1996	2 no digging behaviour	?
arctic char	0 Groot, 1996	1 Fabricius & Gustafson, 1954	?
dolly varden	0 Legget, 1980	1 pers. observations	0 pers. observations
bull trout	0 Groot, 1996	0 pers. observations	0 pers. observations
brook trout	0 Groot, 1996	0 pers. observations	0 pers. observations
cutthroat	1 Groot, 1996	0 pers. observations	0 pers. observations
steelhead	1 Groot, 1996	0 pers. observations	0 pers. observations
masu	0 Groot, 1996	?	?
chinook	0 Groot, 1996	1 pers. observations	0 pers. observations
coho	0 Groot, 1996	0 pers. observations	0 pers. observations
sockeye	0 Groot, 1996	0 pers. observations	1 pers. observations
chum	0 Groot, 1996	0 pers. observations	1 pers. observations
pink	0 Groot, 1996	0 pers. observations	0 pers. observations

Table 19. References for characters 40-42.

	(40) T-d	0=no	(41) und 1	0=no	(42) und 2	0=no
arctic grayling	0	pers. observations	0	pers. observations	0	pers. observations
huchen	?		?		?	
brown trout	0	pers. observations	0	pers. observations	0	pers. observations
Atlantic salmon	0	pers. observations	0	pers. observations	0	pers. observations
lake charr	?		0	Martin & Olver, 1980	1	Groot, 1996
arctic char	?		1	Fabricius, 1953	1	Fabricius & Gustafson, 1954
dolly varden	?		1	pers. observations	1	pers. observations
bull trout	0	pers. observations	1	pers. observations	1	pers. observations
brook trout	0	pers. observations	1	Smith, 1941	1	Butler, 1991
cutthroat	?		0	no literature reports	0	no literature reports
steelhead	0	pers. observations	0	pers. observations	0	pers. observations
masu	?		0	no literature reports	0	no literature reports
chinook	0	Schroder pers. com.	0	pers. observations	0	pers. observations
coho	0	pers. observations	0	pers. observations	0	pers. observations
sockeye	0	pers. observations	0	pers. observations	0	pers. observations
chum	1	pers. observations	0	pers. observations	0	pers. observations
pink	1	pers. observations	0	pers. observations	0	pers. observations

Table 20. References for character 43-44.

	(43) violq 0=yes	(44) wind 0=yes
arctic grayling	?	0 pers. observations (see note 1)
huchen	?	?
brown trout	0 pers. observations	0 pers. observations
Atlantic salmon	0 pers. observations (see note 2)	0 pers. observations
lake charr	?	?
arctic char	0 Fabricius, 1953	?
dolly varden	0 Armstrong & Morrow, 1980	0 pers. observations
bull trout	0 pers. observations	0 pers. observations
brook trout	1 pers. observations	0 pers. observations
cutthroat	?	?
steelhead	0 pers. observations	0 pers. observations
masu	?	?
chinook	1 B. Berejikian pers. com.	0 pers. observations
coho	0 pers. observations	0 pers. observations
sockeye	1 pers. observations	1 pers. observations
chum	1 pers. observations	1 pers. observations
pink	1 pers. observations	1 pers. observations

Notes

1. Grayling females do not build nests, however they perform a probing movement just before spawning that I assumed was homologous to the winding present in other species.
2. I only observed this behaviour in grilse salmon.

Composite Outgroup

A composite outgroup may be used when the relationship among the outgroups is known. It consists in condensing character state information into one line by optimizing characters onto the outgroup phylogeny (Maddison et al. 1984, Wiley et al. 1991, Swofford & Maddison 1992) in order to determine the state of each trait at the outgroup node (McLennan pers. communication).

I have coded my composite outgroup according the following rules:

1. The sister group of the ingroup (*Salmo*) has priority when the decision at the outgroup node is ambiguous (Brooks & McLennan 1991). This implies that whenever the two *Salmo* species had the same character state, and that same state was found within the ingroup, then that value was assigned to the composite outgroup.
2. Whenever the *Salmo* character state was ambiguous (either because it was missing or was a state not present in the ingroup), the state in the other two outgroups was used to determine the outgroup node. However, if one of the two outgroups states was missing the composite outgroup remained ambiguous.

Following the convention of giving the 0 value to the ancestral or plesiomorphic state and 1 to the derived or apomorphic state, I chose the code of each character so that the state was always 0 in the composite outgroup (**Table 21**). This does not imply that the outgroups are “all plesiomorphic”. Characters which are unique to the outgroups (i.e., are not in the ingroup) are uninformative for making polarity decisions. In other words, the outgroups themselves may possess many autapomorphies, and thus are not “all plesiomorphic”, but those traits are not relevant to a reconstruction of phylogenetic relationships in the ingroup.

Table 21. Behavioural-ecological matrix.

Genus	Species	Behavioural-ecological traits								
		1 CI 0 high	2 dac 0 yes	3 dlj 0 yes	4 ds 0 yes	5 fd 0 yes	6 fdd 0 no	7 feed 0 yes	8 fem d 0 yes	9 f-fw 0 never
<i>Thymallus</i>	Arc. grayling	0	?	0	1	0	2	?	1	0
<i>Hucho</i>	Huchen	?	0	?	1	?	?	0	0	0
<i>Salmo</i>	Brown Trout	0	0	0	0	0	1	0	0	0
	Atl. Salmon	1	0	1	0	0	0	0	0	0
composite outgroup	X	0	0	?	0	0	?	0	0	0
	Lake charr	?	0	?	0	?	2	0	1	0
	Arc. charr	?	0	1	1	0	?	0	0	0
<i>Salvelinus</i>	Dolly Varden	?	0	?	1	0	?	0	0	0
	Bull trout	0	0	1	0	0	0	0	0	0
	Brook trout	0	0	0	1	0	0	0	0	0
	Cutthroat	?	0	?	0	0	?	0	0	0
	Steelhead	1	0	1	0	0	0	0	0	0
	Masu	?	0	?	0	?	?	0	0	0
	Chinook	1	0	1	0	1	1	1	0	1
	Coho	1	0	1	0	1	1	1	0	1
	Sockeye	1	0	1	0	1	1	1	0	1
	Chum	1	0	1	0	1	1	1	0	2
	Pink	1	1	1	0	1	1	1	0	2

Table 21. Behavioural-ecological matrix (continued).

Genus	Species	Behavioural-ecological traits								
		10 flex 0 no	11 fnr 0 yes	12 fwpop 0 yes	13 hs-ld 0 no	14 int-s 0 never	15 lc 0 fw 1 amph 2 anad	16 ld-ab 0 no	17 lom 0 no	18 md 0 no
<i>Thymallus</i>	Arc. grayling	0	2	0	0	0	0	0	0	0
<i>Hucho</i>	Huchen	?	?	0	?	0	0	?	0	1
<i>Salmo</i>	Brown Trout	0	0	0	0	0	1	1	0	0
	Atl. Salmon	0	0	0	0	0	2	0	1	0
composite outgroup	X	0	0	0	0	0	?	?	0	0
	Lake charr	?	2	0	?	0	0	?	0	0
	Arc. charr	?	0	0	?	0	1	1	0	0
<i>Salvelinus</i>	Dolly Varden	?	?	0	0	0	1	1	0	0
	Bull trout	1	?	0	0	0	1	1	0	0
	Brook trout	0	?	0	0	0	1	1	0	0
	Cutthroat	?	0	0	0	0	1	?	0	?
	Steelhead	1	?	0	0	0	1	0	1	1
	Masu	?	?	0	?	0	2	?	0	?
	Chinook	?	0	1	0	1	2	0	1	1
	Coho	1	0	1	0	0	2	0	1	1
	Sockeye	1	1	0	1	0	2	0	1	1
	Chum	1	1	1	0	2	2	0	1	1
	Pink	1	1	1	1	2	2	0	1	1

Table 21. Behavioural-ecological matrix (continued).

Genus	Species	Behavioural-ecological traits								
		28	29	30	31	32	33	34	35	36
		ql 0 long	qt 0 I	ra-hs 0 yes	scd 0 yes	semel 0 no	sp-mfw 0 no	sph 0 type I	sq 0 yes	ssp 0 no
<i>Thymallus</i>	arctic grayling	0	0	1	2	0	0	0	0	0
<i>Hucho</i>	huchen	?	?	?	1	0	1	0	?	1
<i>Salmo</i>	brown trout	0	0	0	0	0	0	1	0	0
	Atlantic salmon	0	0	0	0	0	0	0	0	0
composite outgroup	X	0	0	0	0	0	0	0	0	0
	lake charr	?	?	0	2	0	?	2	?	1
	arctic charr	?	?	?	1	0	1	2	?	1
<i>Salvelinus</i>	dolly varden	1	1	1	1	0	0	0	0	1
	bull trout	0	1	0	1	0	0	0	0	1
	brook trout	1	1	1	0	0	?	0	0	0
	cutthroat	?	?	?	0	0	0	1	?	0
	steelhead	0	0	0	0	0	0	1	0	0
	masu	?	?	?	0	1	?	0	?	0
<i>Oncorhynchus</i>	chinook	0	0	0	0	1	0	0	1	0
	coho	0	0	0	0	1	0	0	0	0
	sockeye	0	1	1	0	1	0	1	1	0
	chum	0	0	1	0	1	0	0	1	0
	pink	0	0	1	0	1	0	0	1	0

Table 21. Behavioural-ecological matrix (continued).

Genus	Species	Behavioural-ecological traits							
		37	38	39	40	41	42	43	44
		st 0 fall	tb 0yes	tbd-dw 0 yes	T-d 0 no	und1 0 no	und2 0 no	violq 0 yes	wind 0 yes
<i>Thymallus</i>	Arc. grayling	1	2	1	0	0	0	?	0
<i>Hucho</i>	Huchen	1	?	?	?	?	?	?	?
<i>Salmo</i>	Brown Trout	0	0	0	0	0	0	0	0
	Atl. Salmon	0	0	0	0	0	0	0	0
composite outgroup	X	0	0	0	0	0	0	0	0
	Lake charr	0	2	?	?	0	1	?	?
	Arc. charr	0	1	?	?	1	1	0	?
<i>Salvelinus</i>	Dolly Varden	0	1	0	?	1	1	0	0
	Bull trout	0	0	0	0	1	1	0	0
	Brook trout	0	0	0	0	1	1	1	0
	Cutthroat	1	0	0	?	0	0	?	?
	Steelhead	1	0	0	0	0	0	0	0
	Masu	0	?	?	?	0	0	?	?
<i>Oncorhynchus</i>	Chinook	0	1	0	0	0	0	1	0
	Coho	0	0	0	0	0	0	0	0
	Sockeye	0	0	1	0	0	0	1	1
	Chum	0	0	1	1	0	0	1	1
	Pink	0	0	0	1	0	0	1	1

Matrix and PAUP

The following is the data matrix I used to run PAUP 4.0 b10 following the branch and bound method. The data is entered in the nexus format to facilitate other scientists to repeat, verify or to improve my results as data from missing characters or species become available.

```
#Nexus
begin data;
dimensions ntax=14 nchar=44;
Format symbols="0 1 2" missing=?;
matrix

X
Salvelinus_namaycush      00?00?00000000??00?00000000000000000000000
Salvelinus_alpinus       ?0?0?2010?20?00?00?00100120??020?2?102??01??
Salvelinus_alpinus       ?0110?000?00?01100000000010??1012?101??110?
Salvelinus_malma         ?0?10?000??0001100000000010111100001010?1100
Salvelinus_confluentus   0010000001?000110000000001001010000100001100
Salvelinus_fontinalis    0001000000?000110000000001011100?00000001110
Oncorhynchus_clarki      ?0?00?000?00001?0?100100000??0001?0100?00??
Oncorhynchus_mykiss      1010000001?000101110010100000000010010000000
Oncorhynchus_masou       ?0?0??000??0?02?0?100101001???01?0?00??00??
Oncorhynchus_tshawytscha 101011101?0101201110010100100001001001000010
Oncorhynchus_kisutch    101011101101002011100101101000010000000000000
Oncorhynchus_nerka      101011101110102011111111110101101011000100011
Oncorhynchus_keta        10101110211102201111111110100101001000110011
Oncorhynchus_gorbuscha  11101110211112201111111110100101001000010011;
end;
outgroup X;
begin assumptions;
end;
```

Results

Parsimony analysis of the behavioural-ecological data set produced one single (most parsimonious) tree (**Figure 17**), with the following characteristics:

Tree length = 70

Consistency index (CI) = 0.7571

Homoplasy index (HI) = 0.2429

CI excluding uninformative characters = 0.7424

HI excluding uninformative characters = 0.2576

Retention index (RI) = 0.8534

Rescaled consistency index (RC) = 0.6462 (for definitions of the above parameters, see Wiley et al., 1991).

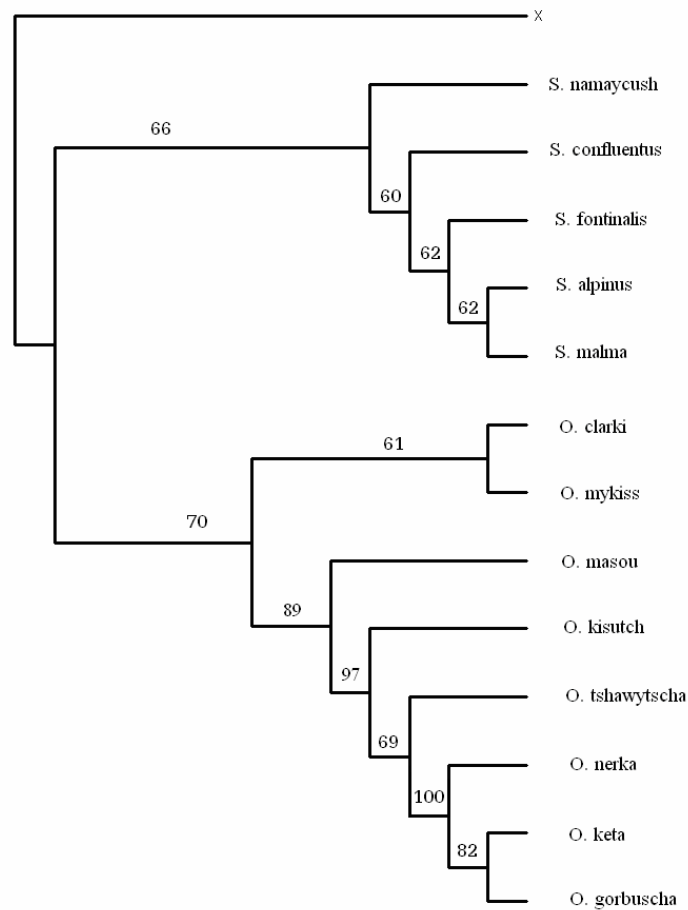


Figure 18. *Salvelinus* and *Oncorhynchus* phylogeny based on MP analysis of forty-four behavioural and ecological traits related to reproduction. Numbers above the branches are the average of 10 independent 100 bootstrap replications.

Discussion

The analysis of 44 behavioural and ecological traits resulted in a solid hypothesis (one single most parsimonious tree) for the evolution of salmonines. There was support for the separation from the ingroup common ancestor into two major well-defined clades (*Salvelinus* and *Oncorhynchus*).

According to my results, the common ancestor of the entire *Oncorhynchus* genus became divided into two separate lineages. One eventually leading to cutthroat and steelhead, the other starting the evolutionary path for the rest of the species. Masu salmon were the first to diverge of this second lineage. Next were coho followed by chinook. Later the line was split into the lineage leading to sockeye salmon and the one leading to the chum and pink clade.

The common ancestor of the *Salvelinus* clade became divided in one evolutionary branch leading to lake charr and other to the rest of the species. Among this second line bull trout were the first to diverge. Next, the line split into brook trout and the lineage leading to the Dolly Varden and arctic charr clade.

This scenario suggests a solution for the consensus tree resulted from references in **Table 2 (Figure 1)**.

Comparisons with other phylogenies

My results showed agreement in various aspects with our current knowledge of the two genera evolution (**Table 2**).

Among *Oncorhynchus*, cutthroat, steelhead and masu were found to be basal to the rest of the members; and the clade formed by sockeye, and chum and pink, was found to be the most recently evolved.

Among *Salvelinus*, my results agree in the basal status of lake charr, bull and brook trout relative to the most novel clade formed by Dolly Varden and arctic char.

There was also agreement in various points with the phylogeny inferred by Crespi & Fulton (2004) (**Figures 2 & 19**). Among *Oncorhynchus*, the following relationships were

congruent: (clarki, mykiss) being basal to the rest of the species, and (nerka, (keta, gorbusha)) being the most recently evolved clade. In addition, the polytomy found on the Crespi & Fulton (2004) tree, was resolved (**Figure 18** versus **Figure 2**). Disagreement came, however, in the relative position of chinook-coho; Crespi & Fulton (2004) reported a sister relationship for both species, while my results positions coho as being basal to chinook. Among *Salvelinus*, agreement was only found in the sister relationship of Dolly Varden and arctic charr.

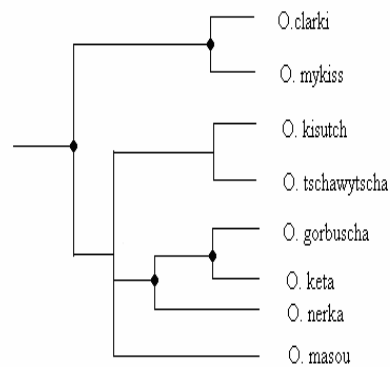


Figure 19. Bootstrap majority-rule based on MP analysis of all nuclear and mitochondrial DNA of Salmonids. Black dots at the branch nodes represent points of agreement with the behavioural inferred phylogeny (**Figure 18**) (redrawn from Crespi & Fulton 2004; only the *Oncorhynchus* species are shown).

The first conclusion of the results is the validity of behaviour as a phylogenetic tool. However, several points make my tree susceptible of criticism.

Firstly, there is a significant number of missing characters for those species I have never observed. These include huchen (20 missing characters), lake charr (15), arctic charr (11), and masu salmon (19). To these we should add cutthroat (13 missing characters), a species on which I have very few observations.

Secondly, bootstrap support, especially for *Salvelinus* species, was relatively low. Apparently, my observations on *Salvelinus* were not enough to have a good resolution for this clade. I had few observations on Dolly Varden and none in lake charr and arctic charr (**Table 1** in **Chapter 2**). Despite there are good literature references describing the spawning behaviour of two of these species (arctic charr and Dolly Varden) no detailed description of

lake charr spawning behaviour exists. Probably, this together with a relative failure in character choosing has resulted in the poor resolution for the *Salvelinus* species. However, most of the published *Salvelinus* phylogenies are incongruent and show a similar lack of resolution (**Figure 1**). The high extent of hybridization present in this genus has been given as an alternative reason to explain the evolutionary uncertainty of this clade (Crespi & Fulton 2004, and references therein).

There are other reasons related to the **MP** theory which makes my results further questionable (discussed below). Despite these concerns, I am going to assume that the species position on my tree is correct and discuss accordingly some of the behavioural trends that may have run during the evolution of this group.

The phylogeny of spawning behaviour

Results using only behavioural traits related to spawning depicted 15 most parsimonious trees (CI = 0.7600). Differences among them were only found on the relative position of cutthroat trout and the sockeye clade. Except for two polytomies, the first one involving cutthroat and steelhead and the second one involving sockeye, chum and pink, the strict consensus tree (Figure 20) was identical to the one including all characters (Figure 18).

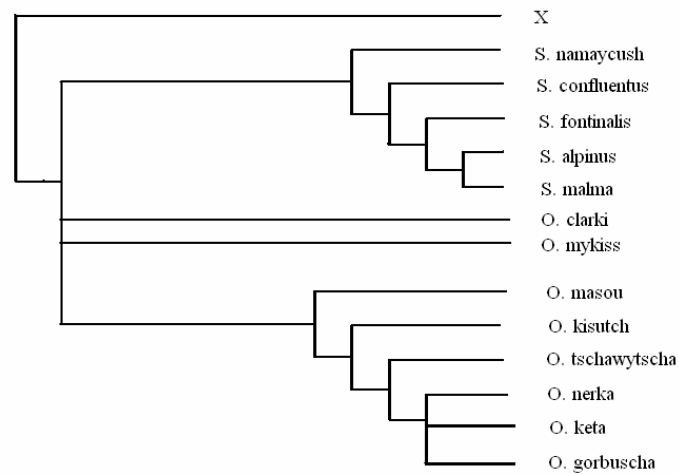


Figure 20. Strict consensus tree based on 33 behavioural characters during spawning.

When analyzing the evolution of behaviour in salmonines several points can be highlighted. There are some behaviours unique to *Salvelinus* not present in *Oncorhynchus* neither in the *Salmo* sister group. These include two distinct types of nest cleaning and egg caring traits (characters 41 & 42) and one distinct type of egg releasing (character 36). In addition, two behaviours related to covering digs (characters 26 & 31) are present in all the species (including the *Salmo* sister group) but not in *Salvelinus*. Two behavioural autapomorphies found on this genus, further distinguishes *Salvelinus* from *Oncorhynchus* (character 8 for lake charr; and 33 for arctic charr). Did all these characters have arisen from new? If the answer is yes, we have to investigate what ecological particularities of the genus may have resulted in the appearance and posterior maintenance of them. Contrary, if we notice the presence of them in any of the two more distant outgroups we have to face an explanation for how these traits were first lost and later reappeared in the charrs common ancestor.

Most probably, a combination of both answers explains the presence of all these unique traits. For instance, Fabricius & Gustafson (1954) indicated that **(und 1)** (character 41) was an adaptation of *Salvelinus* to spawning in still waters (**Chapter 2**). The same is probably true regarding **(und 2)** (character 42). Conversely, the two characters related to the covering diggings (26 & 31), not present in *Salvelinus*, were also reported by Holcik et al. 1988 not to be present in huchen. If we add to these two, the unique presence of character 36 in both *Hucho* and *Salvelinus* we have that at least three of the presumed novel traits present in charr can be explained as reversal evolution (assuming my tree configuration is correct; discussed below).

With regard to *Oncorhynchus*, new behaviours also appeared as this clade was diverging into its actual members (characters 13, 18, 21, 27 & 40). Parallel to these novel changes some other behaviours were lost (7, 18, 22). Overall, a trend towards more advanced parental care took place. *Oncorhynchus* females are the only salmonines that defend their nests until their death. In terms of behaviour, the reproductive effort *Oncorhynchus* females and males overtake during spawning can not be matched by any other salmonine. Most probably, this has been the consequence of a gradual evolution towards semelparity. (Stearley, 1992; McLennan, 1994).

The phylogeny of displays

Ritualized behavioural traits are referred to as displays. Ritualization is the evolutionary process by which a behaviour pattern changes to become increasingly effective as a signal (Wilson, 1975). Due to their stereotypy and consistency among individuals, early ethologists recognized the high phylogenetic value of displays (Tinbergen 1951, 1953 & 1959; Lorenz, 1941a).

Traditionally authors divided displays into fighting and courtship ones; giving more phylogenetic importance to the seconds (Lorenz, 1941a; Tinbergen, 1959). However, as discussed on **Chapters 3 & 4** fighting displays may act as courtship ones (i.e. theoretically females could be seduced by observing male threatening displays) if we assume they are hereditary. Based on that, I have not make distinction between both and included quiverings in the displays analysis. I have also ignored, due to the complexity of measuring it, the frequency by which different species perform displays. For instance, I found that T-displays (character 40) are much more frequent in chum than in pink; or **(hs-ld)**, character 13) is the rule in sockeyes but only seldom can be seen on pinks.

In addition, there are species in which agonistic displays are very common while in others male-male conflicts are mostly resolved by actual attacks. Typically, it can be said that male rivalry in steelhead trout and in Atlantic, coho and chinook salmon most of the times results in actual attacks (pers. observations). In contrast, there are other species like sockeye and pink on which is very common to resolve conflicts by signaling fighting abilities (displays). Chum salmon may be in an intermediate position. The reason for this trend is unknown. Tinbergen (1953), however, predicted that increasing levels of aggression should be accompanied by increased ritualization of agonistic behaviours. With this regard, probably the elevated number of spawners in the later species has resulted in the mentioned differences.

Another possibility that further complicates this trend is a possible relationship between displays frequency and size. I have found that threatening displays are more common in small size species (e.g. brown trout, brook trout) than in larger ones (e.g. chinook salmon, Atlantic salmon). I have also found that within species larger individuals performs less displays than smaller ones. Possible reasons for this relationship may have to do with the relative importance of size versus behaviour before a hypothetical dispute. However, this answer fails to explain the differences between species.

Next, I will discuss individually the phylogeny of some behavioural displays following the phylogenetic theory principle that states:

Never use the characters that are part of the evolutionary hypothesis under investigation to build your phylogenetic tree
(Brooks & McLennan, 1991 p.63)

To further demonstrate the utility of behavioural traits in phylogenetics studies I will also include predictions for what will be the most probable code for a specific display in those species on which I have missing data. These predictions, however, should be taken with caution. They are only hypotheses based on both, the phylogenetic inertia principle and the maximum parsimony concept. They should be understood as educated guesses and cannot be demonstrated before additional research is completed. Whenever this research comes to completion some of the hypotheses will undoubtedly be rejected (as parallel, convergent and reversal evolution exists). However, we can still be certain that a significant percentage of them will be prove to be true (assuming my depicted tree is correct).

Frontal display (fd)

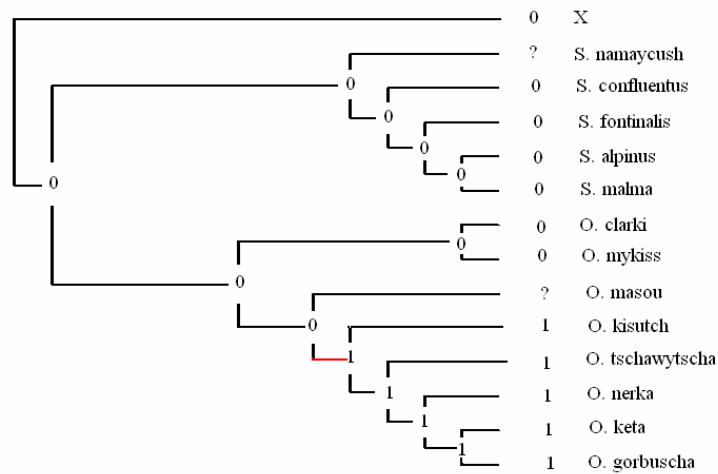
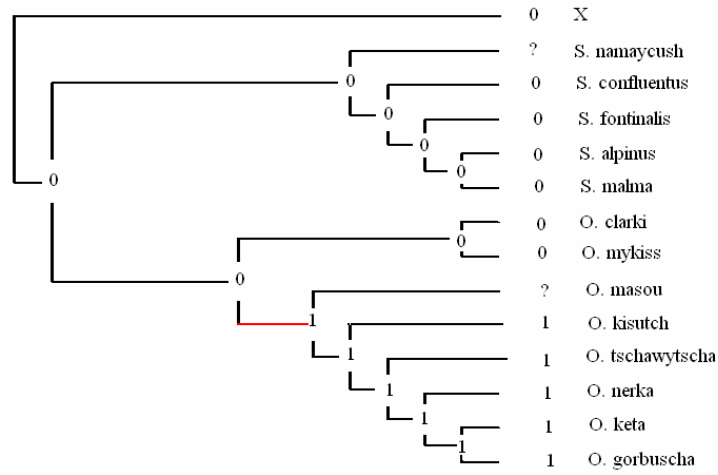
Frontal display is an agonistic behaviour that possibly indicates readiness to fight (**Table 3** on **Chapter 2, Figure 8**). According to my observations, (**fd**) is a plesiomorphic character, present in both members of the sister group *Salmo*, that disappeared somewhere along the lineage leading to the most novel *Oncorhynchus* clades.

When repeating the analysis taking out (**fd**) I got the same one single most parsimonious original tree (CI=0.7536). When mapping this character into that tree two possible scenarios came out (**Figures 21 & 22**). Either the loss of (**fd**) occurred in the common ancestor of the masu or the coho clade.

Independently of when the vanishing of this trait took place, we can predict (**fd**) to be present in lake charr (missing character). Otherwise, it would imply an additional evolutionary change (reversal).

Contrary, the prediction for the other species on which the trait is missing (masu salmon) have two possible outcomes, and thus remains ambiguous. If the loss of (**fd**) occurred in the ancestor of the masu salmon clade we should expect that masu will not perform frontal displays during their male-male confrontations. Conversely, if the ancestor of the coho clade was the one losing this trait we can predict masu salmon to perform frontal displays during male rivalry.

Whenever, along the *Oncorhynchus* lineage the disappearance of (**fd**) occurred the reasons for such vanishing are not known. However, among all the displays discussed on **Chapter 2**, (**fd**) is the only one not having a handicap significance (**Chapter 4**). With this regard, a theoretical discussion about the relative importance of handicap versus non-handicap displays (correlated with the particular species ecology) is recommended (Zahavi & Zahavi, 1997; see **Chapter 4**).



Figures 21 & 22. Two possible hypotheses for the evolution of frontal display in salmonines (0 present, 1 absent). Red branches represent character loss.

High snout-lateral displays (hs-ld)

The high snout-lateral display is a distinct form of the typical lateral display all salmonine species perform (**Figure 12**; see also **Table 3** on **Chapter 2**).

According to my observations, (**hs-ld**) is a derived character that appeared somewhere after the common ancestor of the chinook clade already split into the sockeye clade and the chinook lineage.

When repeating the analysis taking out (**hs-ld**) I got the same one single most parsimonious original tree (CI=0.7647). When mapping the (**hs-ld**) character into that tree, again two hypotheses came out. Either this character appeared in the common ancestor of sockeye and was later loss in the lineage leading to chum; or it independently appeared in the sockeye and chum lineages (**Figures 23 & 24**). Assuming character loss or gain is equally probable; any of those scenarios are just as possible. However, independently of which was the real one, we can predict that lake charr, arctic charr, and masu salmon will not point their snout upwards when performing lateral displays.

The causes explaining the function of this distinct type of lateral display are unknown. Probably, they are related to the evolution of male rivalry in high density spawning conditions. Patrolling waters full of competitors with the body inclined upwards (many times breaking the water surface), can be understood as handicap signaling (see **Chapter 4**). The fact that this trait does not occur in chum salmon can be explained simply because their relative larger size will make most of the times not possible to maintain this position in the shallow waters this species congregate to spawn.

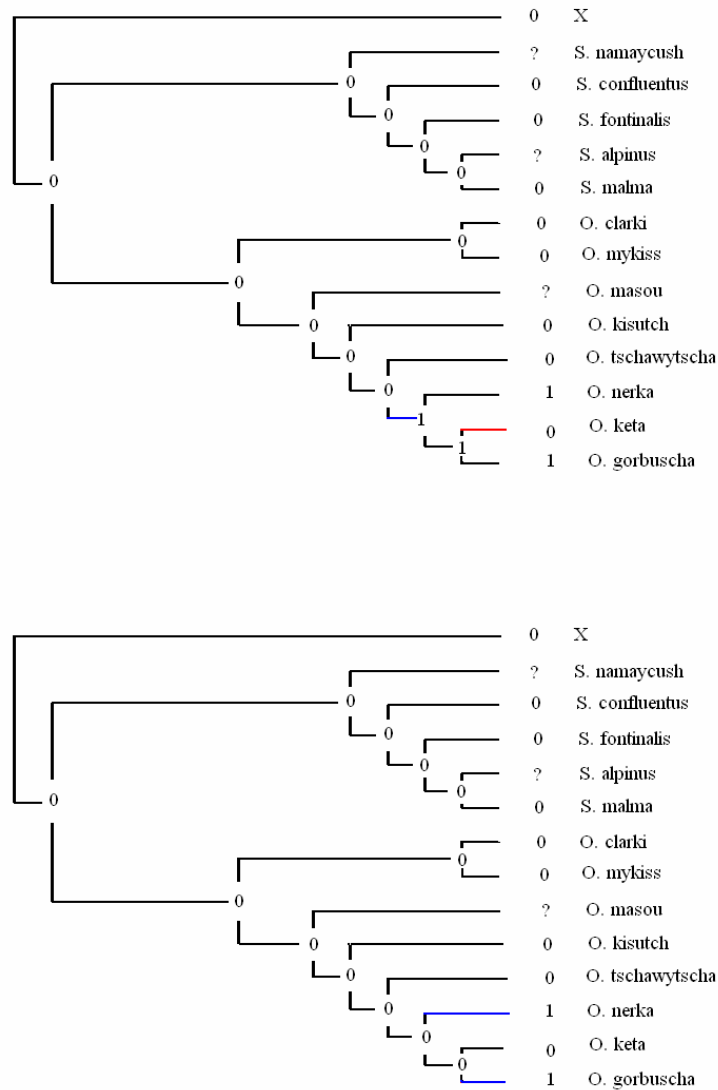


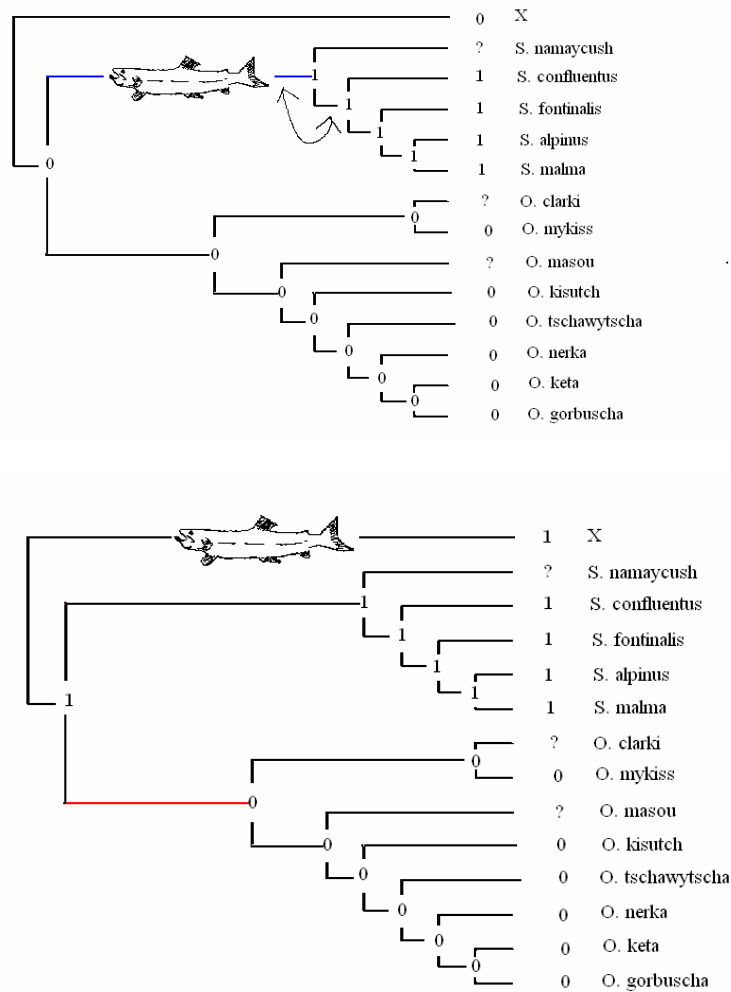
Figure 23 & 24. Two hypotheses for the evolution of high snout-lateral displays in salmonines (0 absent; 1 present). Red branches represent character loss. Blue branches represent character gain.

Lateral displays with arched body (ld-ab)

Again, the **(ld-ab)** character is a distinct type of the common lateral display present in all salmonines (**Figure 13**). According to my observations this trait is ambiguous for the composite outgroup. Atlantic salmon do not arch their bodies during lateral displays, while

brown trout do. To look far down the tree cannot help us to resolve this conflict as this trait is missing in huchen. This leads to two possible outcomes: The trait was either present or absent in the remote ancestor that eventually diverged into the *Salvelinus* and *Oncorhynchus* clades.

When repeating the analysis taking out (ld-ab) I got the same one single most parsimonious original tree (CI=0.7536). When mapping the (ld-ab) character into that tree three possible scenarios can be drawing (**Figures 25 & 26**).



Figures 25& 26. Three possible most parsimonious scenarios for the evolution of (ld-ab) in salmonines (0 absent; 1 present). Blue branches represent character gain. Red branches represent character loss. Arrows indicate two possible locations of character change with equal MP probability.

Independently of whether this trait is plesiomorphic or not, maximum parsimony predicts that cutthroat trout and masu salmon will remain in a horizontal position during their lateral displays.

Male digging (md)

Male digging as a displacement reaction was described on **Chapter 3**. Wilson (1975, p.225), indirectly highlighted the phylogenetic value of displacement reactions when describing them as behaviours *emancipated* from their old functional context.

If I repeated my analysis taking out (**md**) I got the same one single most parsimonious original tree (CI=0.7536). When mapping (**md**) into that tree a unique scenario comes out (**Figure 27**). This allows us to predict that both cutthroat trout and masu salmon males will occasionally unexpectedly dig the gravel with their tails when experiencing escaping-attacking or sexual conflicts (see **Chapter 3**).

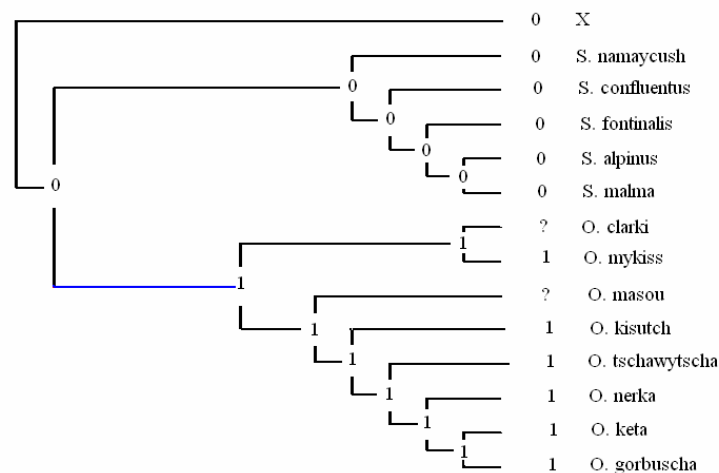


Figure 27. Evolution of male digging in salmonines (0 absent, 1 present). Blue branches represent character gain.

There are species on which (**md**) is noticeably more frequent than in others (**Chapter 3**). However, I decided not to separate this trait into three states because insufficient data and the high number of missing species. Nevertheless, if we had to rely only on my data for converting the binary trait into a multistate one, a trend towards increasing digging, supporting the phylogenetic position of the species, would appear (**Table 22**).

Table 22. Proposed coding for male digging in salmonines (0 absent, 1 seldom, 2 often).

x	lake	arctic	dolly	bull	brook	cutthroat	steelhead	masu	chinook	coho	sockeye	chum	pink
0	0	0	0	0	0	?	1	?	1	1	2	2	2

According to Holcik et al. (1988) huchen males dig their redds to assist females in nest construction. Further research is needed to corroborate this, and in the affirmative case, to distinguish if male digging in huchen is a displacement reaction or a nest building behaviour (parental care).

In any case, if it is true that huchen males dig, the evolutionary history of male digging becomes more difficult to interpret, as two independent changes are needed to explain its present distribution (**Figure 28**).

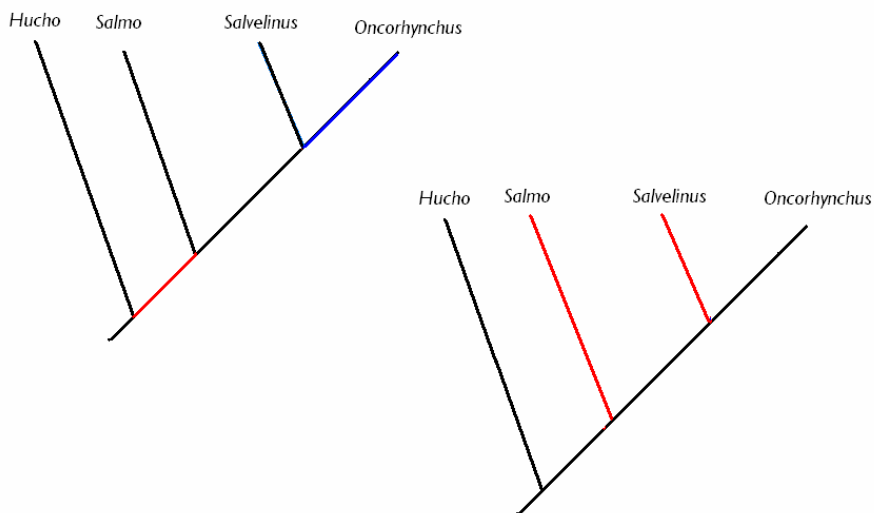


Figure 28. Two hypotheses for the evolution of male digging in salmonines. Red branches represent character loss. Blue branches represent character gain.

T-display (T-d)

T-display is an agonistic display present in chum and pink salmon originally described by Schroder (1973) and proposed on this manuscript as an extreme demonstration of superiority (**Chapters 2 & 4; Figure 16**).

According to my observations, the T-display appeared somewhere when common ancestors of the salmonines most recently clade (chum-pink) were battling on the spawning grounds in their pursue to monopolize females.

When I repeated the analysis taking out (T-d) I got the same one single most parsimonious original tree (CI=0.7536). When mapping the (T-d) character into that tree a unique path for the evolution of this trait appears (**Figure 29**).

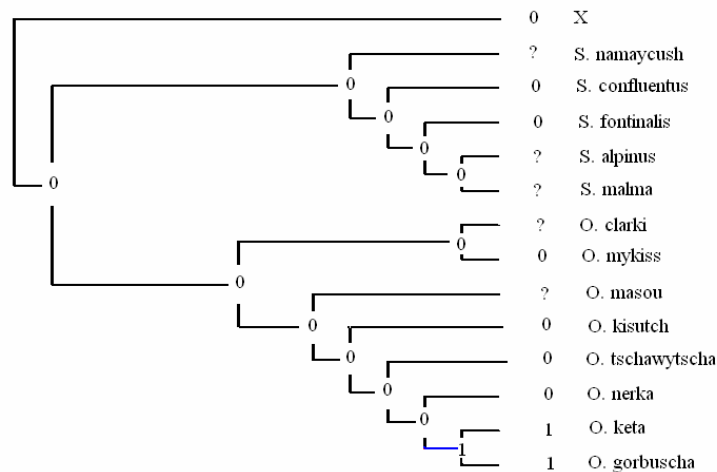


Figure 29. Evolution of T-display in salmonines (0 absent, 1 present). Blue branches represent character gain.

Again, the inferred tree allows us to predict that no males of the following species will demonstrate their superiority by placing their bodies in a perpendicular position against their rivals' snout (see **Chapter 4**): lake charr, arctic charr, Dolly Varden, cutthroat trout and masu salmon.

No interpretation for the appearance of this trait has been done. Probably, causes are again related to crowded spawning areas in where *honest* signaling avoids a number of confrontations (**Chapter 4**).

Quivering type

The frequency and amplitude by which different species perform the typical male courtship display can be differentiated into two distinct types by an underwater observer. There are species on which the quivering is large in amplitude and short in frequency, and others on which both parameters are opposite.

When I repeated the analysis taking out (**qt**) I got the same one single most parsimonious original tree (CI=0.7647). When mapping the (**qt**) character into that tree we have two different solutions that may be resolved when investigators found out if this trait is present in lake charr (**Figure 30**).

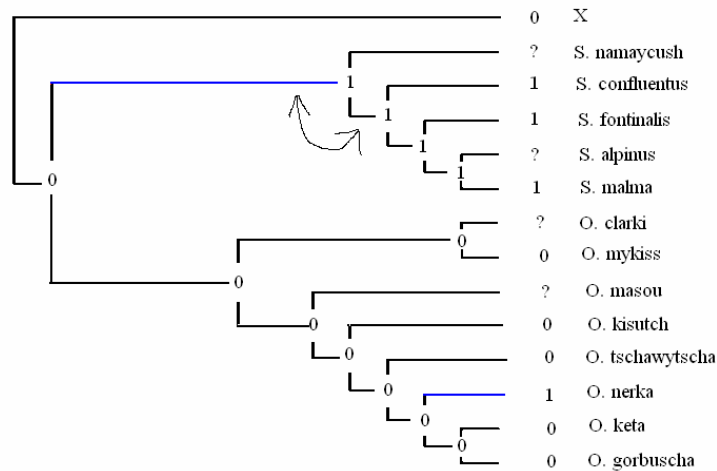


Figure 30. Evolution of quivering type in salmonines (0 type I, 1 type 2). Blue branches represent character change. Arrows indicate two possible locations of character change with equal **MP** probability.

In any of both cases, **MP** theory predicts that arctic charr will quiver their bodies almost imperceptible during the spawning ritual. Instead, the quivers of cutthroat trout and masu salmon males will be conspicuous as they are the one of their closest species.

To resolve why species have adopted these two different paths is a complicated task, as is probably related with each of the species particular physiology. Nevertheless, **MP** theory simplifies this task by highlighting which is the species that has to be subject of comparisons (sockeye salmon).

Violent quiverings (violq)

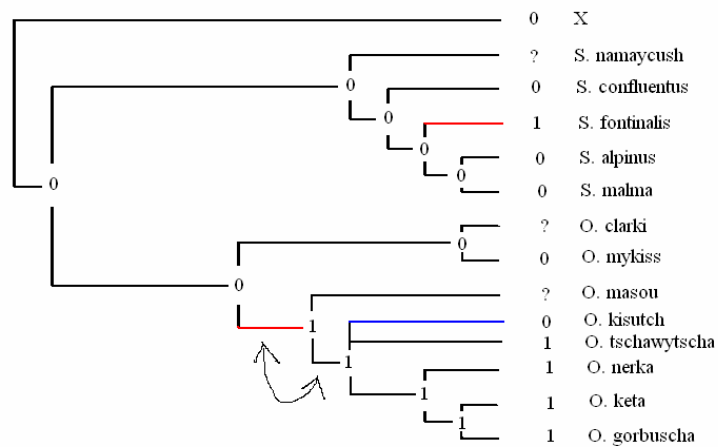
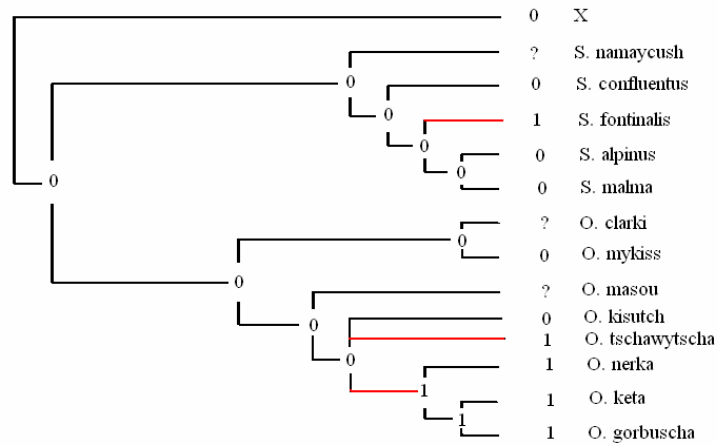
Violent quiverings are probably sexual displacement reactions originated when females do not provide their mates the necessary stimuli to milt release (**Figure 17**; see **Chapter 3**).

According to my observations (**violq**) is a plesiomorphic character that was independently loss in the lineage leading to brook trout and the one leading to chinook and the rest of the species.

When taking (**violq**) out of the analysis I got two most parsimonious trees. The strict consensus tree (CI=0.7647) is identical to the most parsimonious original tree except for the position of chinook and coho (that remains as a polytomy). When mapping the (**violq**) character into that tree three **MP** scenarios can be presented (**Figures 31 & 32**).

Independently, of whose ancestor was the one losing the trait we can predict that both lake charr and cutthroat males will resolve their sexual frustration by unexpectedly shaking their bodies with violence. Contrary we cannot make a reasonable prediction for masu salmon. However, when investigators found out if this trait is present in masu or not we will simplify this trait's evolution eliminating one of the three hypotheses.

Again, why such trait, in some species, has been maintained through evolution relies on physiology and thus we have to assume that the costs of this conspicuous behaviour have been somehow counterbalanced, through evolution, by some unknown benefits.



Figures 31 & 32. Three possible scenarios for the evolution of (**violq**) in salmonines (0 present; 1 absent). Red branches represent character loss. Blue branches represent character gain. Arrows indicate two possible locations of character change with equal **MP** probability.

The phylogeny of the spawning act

According to my outgroup configuration, the ancestral female that was surmounting rivers before the branches leading to *Salvelinus* and *Oncorhynchus* have started to diverge spawned in the most typical Salmoninae fashion (**Chapter 2**). She probably built a series of nests in where she successively laid her eggs. After each deposition, she covered the eggs with beats of her tail. Most probable the later stages of the covering diggings were used to start a new nest and thus the process was repeated over and over, during hours or days, until all her eggs were laid. However, with the appearance of *Salvelinus* a new pattern emerged.

Eventually, research will provide several adaptive answers for the typical manner *Salvelinus* females expel different batches of eggs in seconds (or few minutes) intervals, or for the fact that they do not immediately dig after any of their eggs emissions. However, phylogeny can already provide a valid alternative explanation for them: These behaviours were already present in a common ancestor that probably faced similar ecological problems.

Huchen, considered in this analysis as the second closer outgroup (**Figure 3**), shares with *Salvelinus* this unique form of spawning and egg covering (Holcik et al. 1988; **Table 23**).

Table 23. Character matrix of three behaviours related to the spawning act in four Salmoninae genera. For reasons of consistency, I have reverted the original coding state in some of the characters so all (0) represents absence and all (1) presence.

<i>Genus</i>	Behavioural characters		
	26 psd 0 no	31 scd 0 no	36 ssp 0 no
<i>Hucho</i>	1	1	0
<i>Salmo</i>	0	0	1
<i>Salvelinus</i>	1	1	0
<i>Oncorhynchus</i>	0	0	1

(Characters 26 & 31 are not applicable for lake charr; characters 31 & 36 are opposite for brook trout)..

When mapping these three characters into the tree representing the evolution of the genera *Hucho*, *Salmo*, *Salvelinus* an *Oncorhynchus* an unexpected pattern appears (**Figure 33**).

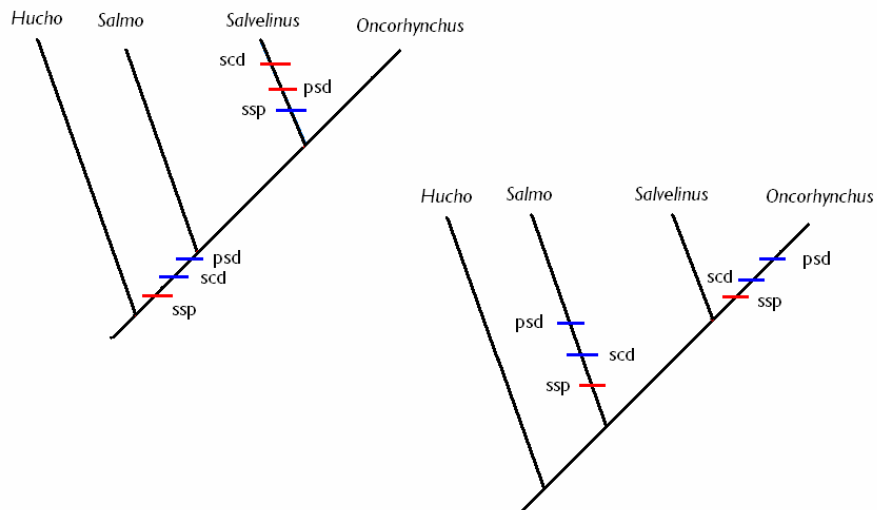


Figure 33. Two solutions for characters change related to spawning act (characters 26, 31, 36). Red dashes represents characters losses. Blue dashes represent character gains.

Six character changes are necessary to explain the evolution of the three characters in the four Salmoninae genera. However, a different more parsimonious solution appears if we interchange the position of *Salmo* and *Salvelinus*. This new representation requires only three character changes and thus is more parsimonious (**Figure 34**).

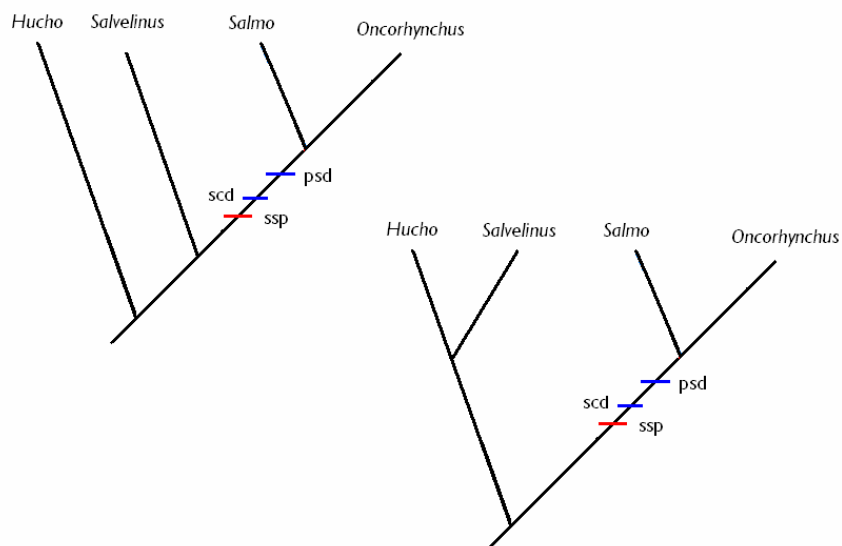


Figure 34. Two alternative hypotheses for the evolution of three characters related with the spawning act. Red dashes represents characters losses. Blue dashes represent character gains.

Furthermore, the fact that one autapomorphy present on my ingroup (character 33 for arctic charr) has been also reported to occur in huchen (Holcik et al. 1988) adds further support for the relation depicted in **Figure 34** and makes questionable the *Salvelinus-Oncorhynchus* sisterhood.

Spawning act duration

The spawning act duration, measured as the initiation of female's gaping and/or trembling until the gaping ends, was a character originally included on this study. However, I was forced to remove it because insufficient data (no statistical test permitted me to assign codes for the species; **Table 24**).

Table 24. Duration of different salmonids spawning act.

Species	duration (sec.)	average
arctic grayling	9, 9, 9, 10, 10	9.67
Atlantic salmon	14, 7	10.5
dolly varden	3,4	3.5
bull trout	6, 4, 3	4.3
steelhead	4, 7, 7, 4, 8,3, 7	6
chinook	9, 11	10
coho	6, 9, 10, 11, 15	10.2
sockeye	10, 11, 9, 16, 9, 10, 9	12.3
chum	9, 12, 14, 14, 14	12.6
pink	4, 6	5

Despite other authors have reported the spawning act duration for several salmonines, the uncertainty of how they were measured stop me for incorporating them into my data (**Table 25**).

Table 25. Spawning act duration of different salmonids. Numbers between dashes indicates ranges; numbers separated by commas indicate individual measures; single number indicate averages.

Species	duration (sec.)	references
arctic grayling	9-25	Beauchamp, 1990
brown trout	1-2	Jones & Ball, 1954
Atlantic salmon	5-15	Jones & King, 1949
lake charr	very brief	Royce, 1951; Martin & Olver, 1980
arctic charr	1-5	Fabricius & Gustafson, 1954
dolly varden	2, 4, 5	Needham & Vaughan, 1952
bull trout	3-6	James & Sexauer, 1997
brook trout	1, <3	Needham, 1961; Power, 1980
chum	10	Schroder, 1980

Nevertheless, I included my observations on this discussion as they may be useful for other scientist when additional data becomes available. Ideally then, we will be able to separate species into those performing long and those performing short spawning acts.

Behaviour and systematics

So far, the individual analysis of the above characters has allowed making predictions for some traits not observed (**Table 26**). .

Table 26. Behavioural matrix. Only predicted codes for missing species are included.

		5	13	16	18	29	39	42
		fd 0 yes	hs-ld 0 no	ld-ab 0 no	md 0 no	qt 0 I	T-d 0 no	violq 0 yes
	lake charr	0	0				0	0
<i>Salvelinus</i>	arctic charr		0			1	0	
	Dolly Varden						0	
	cutthroat			0	1	0	0	0
<i>Oncorhynchus</i>	masu		0	0	1	0	0	

The above predictions, follow the same exact argument **MP** theory uses to build trees. That is, to choose the scenario that requires the minimum number of character changes. A different manner of predicting behaviour relies on an idea that implies the perfect communion between behaviour and systematics.

If a behavioural-based tree is the same or resembles a lot to the tree, others have found using molecular or morphological data we can conclude that the behavioural traits are directly or indirectly related with the molecular/morphological ones. Given that, we can say that by looking the position of a species (never observed by us) in a molecular tree (very similar to our behavioural tree) we can predict with a reasonable degree of certainty what the behaviours of this species will be.

If the above argument is true, one will be able to predict the behaviour of a never observed species provided it has been already classified by molecular or morphological data. This proposal, however, should be taken with caution, for instance in this suggested method there is no way to identify behavioural autapomorphies. Nevertheless, is a good starting point to approach the unknown behaviour of a never observed species.

The phylogeny of life histories

Detailed discussions about the evolution of migratory behaviour and semelparity in salmonids have been reported (Stearley, 1992; McLennan, 1994; McDowall, 1997, 2001; Crespi & Teo, 2002; Hendry et al., 2004; Kinnison & Hendry 2004; Schaffer 2004). Here, I will only make a brief discussion of them, repeating the same procedure done with the above behavioural characters. Instead, I will discuss in detail a life history trait that has received very little attention in the literature: maturity at the parr stage among the *Oncorhynchus* members.

Life cycle (lc)

All salmonines spawn in freshwater; however, there is great variation in the use of this habitat they make (Wilson, 1997). According to a strict composite outgroup analysis we can not know if the ancestor of the ingroup was already traveling back and forth from rivers to the ocean (diadromy), neither we can know if those trips were only related with reproduction (anadromy). However if we examine in detail the outgroup we notice that at its node only two outcomes are possible (amphidromy & anadromy; **Figure 35**). If we look further up the tree we see that all the species in one of the ingroup clades are non-anadromous (*Salvelinus*). Furthermore, all the clades only have in common the amphidromy character. Therefore, I have opted to consider amphidromy to be the original life history of the ingroup common ancestor.

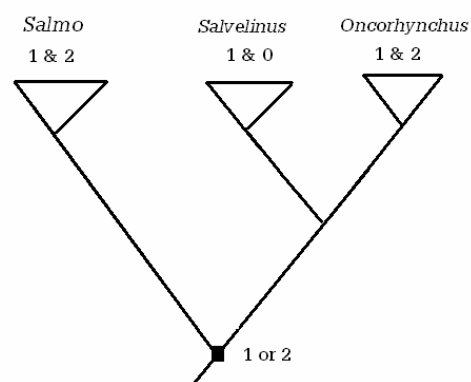


Figure 35. Hypothesis for the evolution of salmonines life cycle regarding their migratory behaviour (0 freshwater, 1 amphidromy, 2 anadromy).

When repeating the analysis taking out (**lc**) I got the same one single most parsimonious original tree (CI=0.7500). When mapping the (**lc**) character into that tree, assuming amphidromy was the plesiomorphic condition, a unique scenario appears (**Figure 36**).

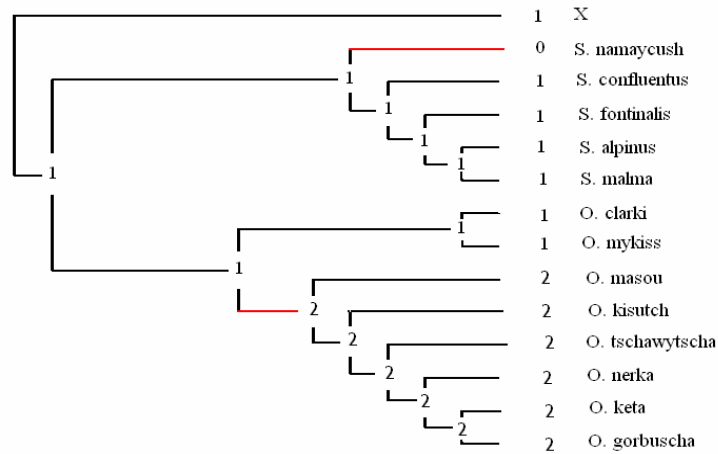


Figure 36. Hypothesis for the evolution of migratory behaviour in salmonines (0 freshwater; 1 amphidromy; 2 anadromy). Red lines represent character change. Species that have both anadromous and freshwater populations were considered anadromous. Species that have both anadromous and amphidromous populations were considered amphidromous.

Anadromy evolved in the lineage leading to masu and the rest of the species. Lake charr independently lost the faculty, which all the other species have, for visiting seawaters.

However, if we include in the analysis the *Salmo* outgroup we necessarily arrive to the conclusion that anadromy has independently evolved twice in the *Oncorhynchus* and *Salmo* genera (see **Figure 35**).

Semelparity (semel)

According to my outgroup configuration the *Salvelinus* and *Oncorhynchus* common ancestors were dividing their chances of having a successful reproduction in at least two events during their lifetime (iteoparity).

When I repeated the analysis taking out (semel) I got the same single most parsimonious original tree (CI=0.7536). When mapping the (semel) character into that tree a unique evolutionary MP hypothesis appears (Figure 37).

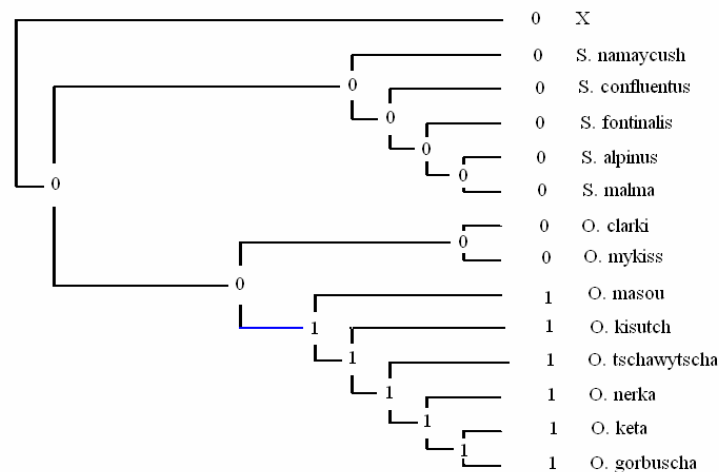


Figure 37. Hypothesis for the evolution of semelparity in salmonines (0, absent; 1 present). Blue line represents the fixation of semelparity.

Semelparity evolved once, in the common ancestor of the six species of Pacific salmon. However as stated by Stearley (1992), semelparity in salmonines should be understood as a continuous trend from different degrees of iteoparity to extreme semelparity (see Fleming 1998). The fact that some populations of masu salmon, (as well as chinook parr in laboratory conditions; **Table 16**), have survived spawning corroborates this idea.

Parr maturation in Pacific salmon (pm)

Precocious maturation at the parr stage is common in *Salmo* and *Salvelinus*. It also occurs in Pacific trout and in some of the Pacific salmon (**Table 3 in Chapter 1**). However, especially in the later is less common and has not been studied in detail.

The fact that male parr maturity occurs in almost all the salmonines unequivocally implies that is a trait inherited from ancestral species. Ecological differences probably have resulted in the gradual lost of **pm** by Pacific salmon. If this statement is true, we should consider some of the possible causes driving this progressive decline.

Firstly, Pacific salmon are semelparous species, characterized by a tremendous investment in one single lifetime reproductive event followed by death (Fleming, 1998; but see **Table 14** for exceptions). Semelparity is thought to have evolved because of extreme anadromy when species overcome long-distance migrations between feeding and spawning grounds (Unwin et al., 1999; Crespi & Teo, 2002). Probably, the endocrinology role of semelparity (Stearley, 1992) plus a trade off between offspring survival and spawner mortality has conditioned the disappearance of early maturity. However, the fact that there are semelparous species with maturity at the parr stage (masu and chinook) indicates that semelparity was fixed before this trait disappeared.

Secondly, Pacific salmon are known to spawn in massive densities. This occurs when overwintering fish return to spawning grounds in tight synchrony (Stearley, 1992; Fleming, 1998). The levels of aggressions are known to increase dramatically as a function of density (Van den Berghe & Gross, 1986). Additionally, adults of both sexes are known to attack juvenile fish in the redds (Garcia de Leániz, 1990; Tsiger et al., 1994; **Table 2 on Chapter 2**). Given that the main tactics of precocious males is to sneak into fertilizations, probably the effect of crowded spawning areas (diminishing the available refuges for parr) has resulted in a behavioural selective force against precocious maturation. In favor of this, we have that parr maturation is present in the species in which the spawning aggregations are not so massive (i.e. chinook and masu).

Thirdly, and probably most important, only species having a long freshwater residence time during their juvenile stage can maintain this strategy. In order for a juvenile fish to become a precocious male, he needs the necessary time for growing to a minimum size. In addition, he needs to remain in freshwater at least until the anadromous females make their return back to the spawning grounds. Unsurprisingly, parr maturation has never been reported in pink and

chum salmon known to enter seawater soon after their emergence from gravel. However, sockeye salmon poses a problem because they reside in freshwater (lakes) for long periods before entering the ocean yet they do not mature at the parr stage.

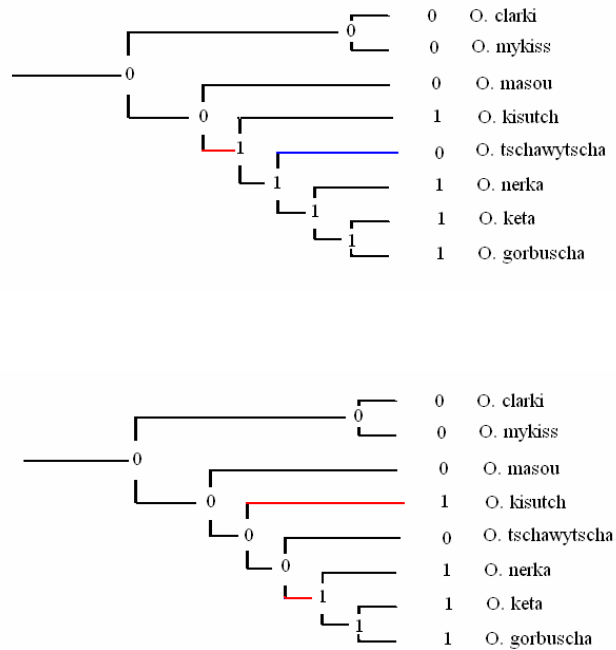
A suggested manner to study if the three discussed parameters have significance on early maturity is to use them to predict whether species will have **pm** or not. **Table 27** combines the three parameters with the prediction for maturity at the parr stage. The effect of each parameter is assumed to be equal and is indicated with + and – signs (favoring or disfavoring maturity).

Table 27. Absence (0) and presence (1) of three different life history parameters among *Oncorhynchus* species. The (+) sign is presumed to favor precocious maturation while the (-) one disfavors it.

	semelparity	massive spawnings	long freshwater life	total	predictions for parr maturation
cutthroat	0 (+)	0 (+)	1 (+)	+++	1
steelhead	0 (+)	0 (+)	1 (+)	+++	1
masu	1 (-)	0 (+)	1 (+)	-++	1
chinook	1 (-)	0 (+)	1 (+)	-++	1
coho	1 (-)	0 (+)	1 (+)	-++	1
sockeye	1 (-)	1 (-)	1 (+)	--+	0
chum	1 (-)	1 (-)	0 (-)	---	0
pink	1 (-)	1 (-)	0 (-)	---	0

The real presence of **pm** agrees the predictions except for one species. This is the coho salmon. This species has a long period of residence in freshwater and does not spawn in such big densities as others (i.e. sockeye, chum and pink) yet maturation at the parr stage among them has never been cited.

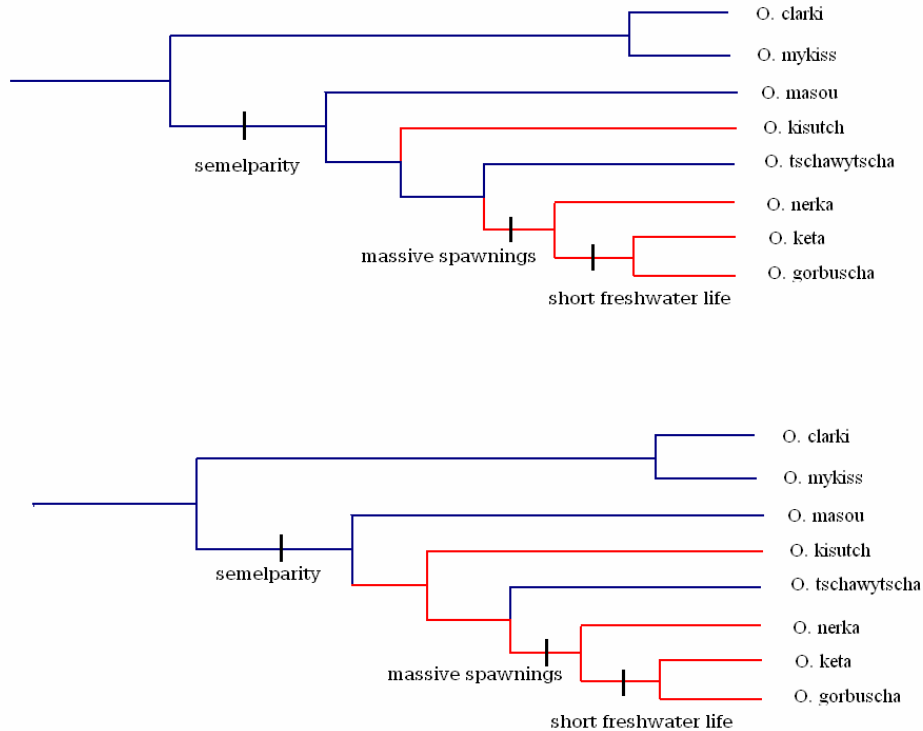
Phylogenetic analysis via outgroup comparisons provides a visualized alternative method to study the effect on (**pm**) of the above variables. If we first repeat the analysis taking out (**pm**) we will get the same one single most parsimonious original tree (CI=0.7761). When mapping the (**pm**) character into that tree two solutions are possible (**Figures 38 & 39**).



Figures 38 & 39. Two hypotheses for the evolution of precocious maturation in *Oncorhynchus* (0 present, 1 absent). Red branches represent the loss of precocious maturation. Blue branches represent the gain of precocious maturation.

Either precocious maturation was lost in the clade leading to coho and the rest of the species and later reappeared in the lineage leading to chinook, or it independently disappeared in the lineage leading to coho and the one leading to sockeye and the remaining species.

If we now, re-run the analysis taking out the tree parameters on **Table 27** (characters 9, 21 & 32) plus the (**pm**) trait (character 25) we will get the same original tree (CI=0.7705). When mapping all the characters into that tree results confirm that none of the parameters has a definitive effect (**Figures 40 & 41**).



Figures 40 & 41. Evolution of precocious maturity at the parr stage (pm) in *Oncorhynchus*. Blue branches represent lineages with (pm). Red lines represent lineages that have lost (pm). The appearance of semelparity, massive spawnings and the disappearance of a long freshwater life is mapped on the trees.

After semelparity was fixed two evolving lineages maintained this strategy (masou and chinook). Before both, massive spawnings and short freshwater life, were fixed one lineage loosed the ability to mature at the parr stage (coho).

This leads to several possibilities:

- 1) My depicted tree is wrong, and consequently we cannot infer the relative importance of any of the parameters.
- 2) There is another unknown trait that caused the disappearance of **pm**.
- 3) Some coho male parr do mature at the parr stage.

Further research is needed to explore the third possibility. During my observations of spawning coho I have frequently seen numerous parr in the redd vicinity. The classical explanation for this fact is that those are parr waiting for the spawning act to prey on eggs. However, until more studies are done we cannot rule out the possibility that some of them are sexually mature.

Future Research

This project constitutes the first approach to a partial Salmoninae phylogeny based only upon behavioural and ecological traits. The study that can be repeated and improved by other scientists adding new species or further investigating the presence of many of the missing traits (or adding new ones). Ideally, this could lead to a clear and robust phylogeny hypothesis for the entire subfamily based only on behaviour.

However, before this task can be completed, a long and difficult way has to be undertaken. There is a historical research gap for the trout species that live and spawn in streams across the mountain ranges of Southwest USA and Northwest Mexico. Most of the publications referring to the spawning behaviour of masu salmon are written in Japanese and are not available to the broad scientific community. Behaviours of the three species belonging to the *Hucho* genus are largely unidentified. Except, for a reference by Holcik 1982, stating that lenok females do not built nests, the behaviour of this freshwater fish from the *Brachymystax* genus remains virtually unknown. The spawning habits of the commonly named archaic trouts (placed in the genera *Platysalmo*, *Salmothymus* and *Acantholingua*) remain a mystery even for the more dedicated ichthyology journals.

Research in many of these species has been long neglected because difficult access or political problems in the areas they inhabit. Probably as this trend is reverted and research arrives to isolated mountain ranges of former URSS and Mongolia new species will be discovered. Eventually we will have a complete picture of the behavioural ecology of this group of fish. We then, may be able to answer whether lenok performs the characteristic undulating movements *Salvelinus* females do or whether the quiverings of apache trout are conspicuous like the ones of most of the members of their genus.

Overall, my results have found a remarkable similarity with Salmoninae phylogenies based on molecular and/or morphological data, supporting the idea of behaviour's utility as a phylogenetic tool. However, why should we use behaviour instead of molecules?

Genes can only tell us how relatively far apart species are. Only devoted observations and behavioural recordings, can lead to a well-built hypothesis for the evolutionary history of this group of fish. Only by acquiring this knowledge, we will be able to apply it to manage the declining populations of salmonines.

Theoretical criticism

MP states that the most likely scenario involves the fewest number of changes. However, that assumption implies a perfect efficiency in the evolutionary process that is at least questionable (see Hall, 2001). Furthermore, the arguments here presented have assumed a model of evolution by which 1 ancestral species leads to two new species (cladogenesis). However, the formation of new species through the hybridization of two ancestral species (reticulate speciation) may have also played an important role in the salmonines evolution (see Taylor, 2004).

According to the maximum parsimony concept the closer the **CI** is to one in a phylogenetic tree the most accurate it is. However, to expect such behavioural conservatism in species that have diverged millions of years ago and have been exposure to variable environmental pressures is unrealistic.

How, if not, can we explain the intriguing similarities between two so distant species like (some populations of) sockeye salmon and lake charr? They both spawn in freshwater lakes and use this habitat as nursery for their young. Some sockeye females, the same as all the lake charr ones, spawn without digging redds (Wilson, 1997). The male quiverings of all the sockeye males are amazingly similar to the ones other *Salvelinus* members perform. Yet their evolutionary lineages separated millions of year ago before any of the actual *Oncorhynchus* and *Salvelinus* existed.

How, if not by convergent evolution, can these two species be so close and so far?