

Lake trout (*Salvelinus namaycush*) spawning behaviour: the evolution of a new female strategy

Manu Esteve · Deborah A. McLennan ·
John M. Gunn

Received: 4 December 2006 / Accepted: 2 July 2007
© Springer Science + Business Media B.V. 2007

Abstract A video camera inside an underwater housing was used to record the spawning activities of lake trout, *Salvelinus namaycush*, in Kushog Lake, Ontario (Canada). Contrary to the commonly accepted belief describing lake trout as the only salmonine to spawn exclusively at night, the recordings were taken during the day. Lake trout spawning behaviour is described in detail and compared with other salmonine species. The loss of female “nest-building” and assumption of a novel itinerant strategy during which females travel across the breeding grounds accompanied by a group of males, is considered to be an important change in the evolution of the lake trout’s unique mode of spawning.

Keywords Underwater video · Evolution · Salmonines · Sexual selection

M. Esteve (✉) · D. A. McLennan
Department of Ecology and Evolutionary Biology,
University of Toronto, 25 Harbord St,
Toronto, Ontario M5S 3G5, Canada
e-mail: manuesteve@zoo.utoronto.ca

J. M. Gunn
Cooperative Freshwater Ecology Unit Biology Department,
Laurentian University, 935 Ramsey Lake Road,
Sudbury, Ontario P3E 2C6, Canada

Introduction

Salmonine fishes have been studied extensively for decades, so it is perhaps surprising to discover that the description of the spawning behaviour of the lake trout, *Salvelinus namaycush*, is still relatively absent from the literature. For example, Esteve and McLennan (2007) used *Salvelinus* as an outgroup in their behaviour-based analysis of phylogenetic relationships within *Oncorhynchus* (Pacific salmon and trout). At the time their manuscript was written, most of the characters for lake trout had to be coded as “unknown”. This dearth of information is generally attributed to the lake trout’s propensity to spawn only at night and to shun areas lit by artificial light (Gunn 1995), making it difficult to observe in either the field or the laboratory. It has thus been more practicable to collect data about the physical factors influencing timing and duration of spawning or the choice of a spawning site (e.g., Martin and Olver 1980; Liimatainen et al. 1987; Gunn 1995) than to document the actual behaviours performed from arrival on the breeding grounds to gamete release.

Our knowledge about lake trout spawning, which is based largely on observations appended to larger ecological studies (Royce 1951; Martin 1957; DeRoche 1969; Watson 1999), can be summarized as follows: fish show a tendency to return to the same spawning areas every year in the fall, suggesting homing behaviour, as is the norm in other salmonines.

Males are the first to arrive on the breeding grounds, where they can be seen swimming at nearly any hour of the day or night, waiting for females to appear. They tend to spend daylight hours offshore in deeper water, moving shoreward as light levels drop. Once the females arrive, which often coincides with periods of heavy winds, fish begin to congregate in groups, swimming slowly (traveling) over the coarse gravel substrate found along the wind swept lake margin. Breeding activity peaks between dusk and midnight, during which time one or more of the males surrounding a female will brush along her flanks, nibbling at her fins. Eventually gametes are released, accompanied by both partners gaping and raising their dorsal fins. Spawning activity can be concentrated in as few as two to three nights or spread over 2–3 weeks, depending upon environmental conditions.

Even this sketchy description highlights several major differences between the spawning behavior of lake trout and other salmonines. For example, lake trout appear to be the only salmonine that (1) spawn without building a nest (Martin and Olver 1980). Instead of establishing and defending a territory, females wander across large areas, intermittently laying batches of eggs over selected substrate crevices. Not surprisingly, females show none of the territorial behaviours common in other species (Esteve 2005b); (2) lack overt male–male competition (Gunn 1995; Watson 1999); (3) lack distinct sexual dimorphism such as differences in body colour or snout restructuring; and (4) limit its breeding activities almost entirely to periods of darkness (Gunn 1995). Although these differences are well documented in the literature, no one has tried to delineate the factors that may have been involved in the evolution of the lake trout's unique spawning repertoire. Our goals in this paper are thus two fold. First, we report detailed descriptions of the behaviours leading to gamete release based on underwater video recordings of lake trout spawning in the wild. Second, we use these new data to investigate the evolution of the lake trout spawning repertoire. These data will be useful to both systematists interested in reconstructing phylogenetic relationships within the Salmoninae in general and *Salvelinus* in particular, and to biologists interested in managing this economically important resource.

Materials and methods

Study area

Spawning events were recorded on 6 November 2005 at Kushog Lake, Southern Ontario (45°05'40" N; 78°47'34" W). Kushog Lake is a 640 ha oligotrophic lake (max. depth 38.1 m, mean depth 9.9 m) with a healthy lake trout population. The spawning section consisted of approximately an area of 10 m in length and 2 m in width paralleling the shore (Fig. 1). Substrate was composed of coarse gravel mixed with rubble and rock. Spawning depth fluctuated between 0.1–0.5 m, with the majority of spawning events observed in shallow waters of less than 0.3 m. High winds and intermittent rain throughout the day reduced underwater visibility by stirring up a substantial amount of suspended material, which may explain why spawning started during the day rather than at night. This explanation is supported by seven

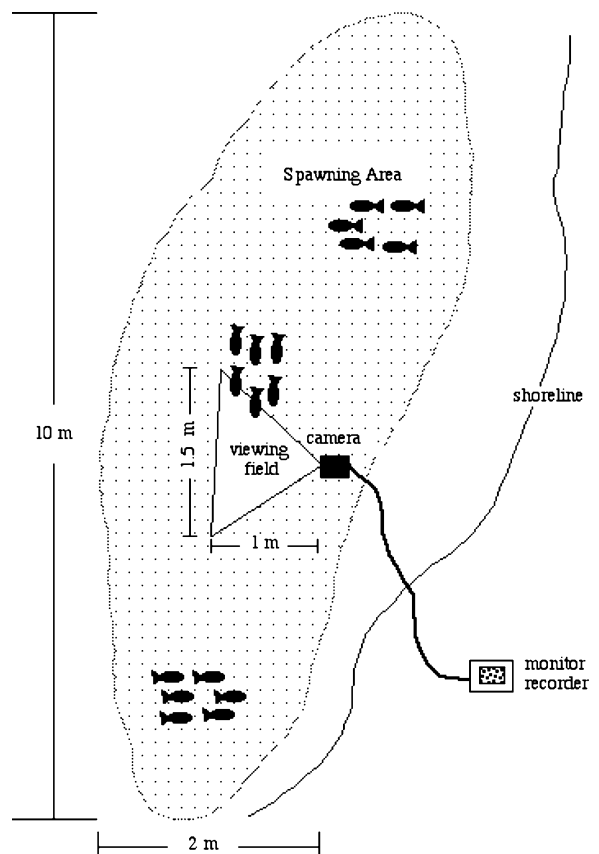


Fig. 1 Diagram showing the spawning area and camera settings. Not drawn to scale, distances are visual approximations as no direct measurements were taken



Fig. 2 A camera inside a housing records lake trout activities. Notice the gravel substrate common to spawning grounds

futile attempts to record spawning at the same location when the water was clear (2005: October 23, 30; November 5, 12. 2006: October 21, 27; November 3).

Underwater video recordings

A colour mini DV camera (Sony TRV 900), bearing an angular lens ($\times 0.5$) was mounted inside an acrylic housing and placed in 0.3 m of water approximately 2 m from the shore (Figs. 1 and 2). The video signal was transmitted via cable to a mini DV digital video cassette recorder (Sony GV-D900E). Images were recorded using a remote commander (Sony RM 95) that allowed manual zooming and focusing from shore. The camera remained in a stationary position for

the entire recording period. Poor visibility restricted the capture of clear images of lake trout to approximately 1 m from the camera; lateral view range was estimated to be approximately 1.5 m (Fig. 1). Since lake trout have no overt morphologically based sexual dimorphism, we used behaviour to identify males and females. Specifically, a female was identified as the fish at the front of a small group, constantly followed by one or more fish scored as males because they performed quivering bouts along the lead fish (a typical male salmonine courtship behaviour consisting in low amplitude and high frequency body vibrations from head to tail; Esteve 2005b). It was impossible to identify individual males or females. Visible sperm clouds and, in some cases, eggs were used as an unequivocal signal of gamete release.

Results

A total of 10 spawning acts were recorded within range of the camera (Table 1). Males were seen wandering throughout the spawning area when the observations started at 11:00. Actual spawning activities began around 12:45 when several females approached the area and crossed over it. At this point, one or more males rapidly pursued each female at a close distance. The female invariably responded to these sudden approaches by fleeing into deeper parts of the lake. At approximately 14:00 females began to stay in the spawning area, allowing any male to approach them. From this time recordings started and

Table 1 Notes from the 10 recorded spawning acts for lake trout in Kushog Lake

Spawning number	Number of males with female	Notes	Time
1	4	Only two males were seen gaping	15:45:07
2	5	Spawning only involved the two males adjacent to the female's sides; three other males were circling above	15:55:41
3	5	Only the male in front of the camera was seen to quiver and gape	16:01:52
4	5	Female was seen quivering; one male did not participate	16:02:42
5	4	Only the two adjacent males seem to participate, males move forward during sperm release	16:10:09
6	4	3 males were seen gaping	16:17:09
7	5	3 males appear to participate in the spawning	16:30:27
8	5	Only 1 male appears to participate, the other 4 males were circling above	16:34:45
9	6	Not possible to determine how many males participate	16:38:14
10	6	Not possible to determine how many males participate	16:40:57

continued until 17:00, when light levels were too low to be detected by the video camera. All the recorded spawning events were concentrated in a 1 h period. It was not possible to determine how many individual females were filmed during that time because the fish were not tagged.

Courtship generally progressed as follows: a female slowly swam in large circles over the spawning grounds with a variable number of males (1–7) following her from between three to one half fish lengths away. Eventually two males started to brush and nibble the female's vent region (Fig. 3), then began rubbing along opposite sides of her body. These males often swam beside her, nipping and nudging her sides with their heads and snouts. Over time males began to quiver the female. She responded by either continuing to travel with no apparent alteration of swimming speed or vertical position, or by stopping and sinking to the bottom (Fig. 4). In the latter case, the males who were quivering her always stopped and sank with her, continuing to quiver. Of the remaining males, the ones closest to the quivering trio also sank, retaining their distance, while males furthest away tended not to sink. At this point, the entire group of fish appeared to drift slightly forward due to inertia; no movement of their tails was recorded. Once on the bottom, the female either resumed travelling or spawned. In the latter case, males that did not sink began swimming slowly above and around the spawning group. Prior to a spawning act, the female raised her caudal fin and started to



Fig. 3 A lake trout female followed by three males (one of the males is on the female's opposite side). Observe one of the males brushing the female's lateral side with his snout



Fig. 4 A group of lake trout sinking to the bottom just seconds before gamete release. First fish is a male, second one is a female and the last four are males

quiver her body. The two males who had been quivering her responded by assuming the typical salmonine spawning position, arching their quivering bodies, tails pointing upwards and jaws agape (Fig. 5). Non-quivering males near the spawning female often (but not always) displayed the spawning arch-gape as well. At the point of gamete release, males inclined towards the female with extended pelvic and dorsal fins. Although the act itself was very brief (1–2 s), it was easily detectable because a male accelerated forward and slightly upwards while releasing sperm. Using this as a criterion for spawning, it appears that any male who had sunk with, and quivered, the female, was involved in releasing sperm



Fig. 5 Lake trout spawning group during gamete release. First fish in the bottom is a male, the female is the fish to his right side. The fish above is a male that failed to synchronize with the spawning position

during the spawning act. Immediately after a spawning event, the fish resumed their traveling and courtship activities.

Overall, lake trout spawning was composed of a sequence of three distinct behaviours (Fig. 6): (1) traveling: the female slowly swims with one or more quivering males in parallel and slightly behind her. (2) sinking: the female and the males accompanying her stop swimming and sink to the bottom while the males continuing quivering. (3) spawning: release of gametes while female and males quiver and gape their jaws. A total of 27 quivering acts were recorded, 20 of which involved the participants sinking to the substrate. Of those, ten resulted in spawning, and the other ten were followed by the resumption of traveling. The other seven quivering bouts were observed from the shore, but it was not possible to assess whether any of them ended in a spawning event. During the entire period we did not observe substrate digging or any agonistic interaction among the group of males following the female. After spawning, females did not perform any behaviours indicative of egg covering or caring, but rather resumed traveling.

Discussion

The use of a remote underwater video camera, coupled with the fortuitous discovery that lake trout will spawn during the day if the water is sufficiently cloudy, has allowed us to fill in much of the missing data concerning lake trout breeding behaviour. Observations based on 10 separate spawning events indicate that: (1) female sinking to the bottom followed by tail raising is an unambiguous signal that gamete release is imminent; all 10 sink+tail raise episodes were followed by the spawning act; (2) lake trout move

forward during gamete release, something that has only been previously recorded for brook trout, *Salvelinus fontinalis* (M. Esteve, unpublished observations), arctic charr, *Salvelinus alpinus* (Fabricius and Gustafson 1954) and huchen, *Hucho hucho* (Holcik et al. 1988); (3) the spawning act is brief, lasting 1–2 s. This is similar to other members of *Salvelinus* and differs from Pacific salmon and trout (*Oncorhynchus*) species, in which gamete release lasts anywhere from 4–16 s (Esteve 2005a); (4) there is no intentional cleaning of egg deposition areas prior to spawning (with the exception of one male picking an undetermined particle from the substrate. Particle picking was also previously reported by DeRoche (1969) and Gunn [unpublished observations]). The presence of numerous fish in the shallow area, accidentally brushing the bottom with their bodies or sweeping over it during swimming did, however, cause an inadvertent cleaning of debris from the substrate. (5) Although neither males nor females displayed any of the recognized suite of salmonid agonistic behaviours, we did notice from the shore that normal traveling occasionally ended in abrupt splashes, indicating possible disputes between either the males and the female or among males. (6) Contrary to the other members of the *Salvelinus* genus, lake trout females do not perform any egg caring behaviours after spawning.

During this study we observed seven quiverings from the shore when the fish were in shallower areas. This behaviour generated high frequency vibrations at the water surface, producing a distinguishable sound, as well as bubbles and traveling waves. In a study with *Salvelinus fontinalis* × *S. namaycush* hybrids, Berst et al (1981) reported that different sound frequencies were associated with distinct behaviours such as female diggings and pair spawning quiverings. Salmonids are thought to have very poor hearing—they are only

Fig. 6 Diagram showing the lake trout spawning behavioural sequence. Arrows indicate the direction of movement



capable of detecting low frequency sounds at relatively high intensities (e.g. Hawkins and Johnstone 1978; Schellart and Popper 1992)—so it is unlikely that conspecific males will be attracted to quivering vibrations based on the acoustical aspect of those cues. If the vibrations are within the range of detection by the lateral line, however, then quivering could alert conspecific males in the vicinity to the presence of a sexually receptive female. This has special relevance for lake trout males because females do not advertise their receptivity by visual, and possibly vibrational cues associated with digging, so any attraction that occurred would result solely from the males' own quivering behaviour. Further studies are needed to determine whether such attraction does indeed occur because, if it does, it will represent a cost to quivering; a cost that would be predicted to fluctuate in intensity depending upon the sex ratio and the density of surrounding males in the spawning area.

The spawning behaviour of lake trout differs dramatically from other salmonines but it is extraordinarily similar to that exhibited by coregonines. Whitefish spawn at night, do not defend territories or build nests, spawn promiscuously without any signs of male–male competition (Fabricius and Lindroth 1953) and do not display any overt morphologically or colour-based sexual dimorphism. How did the lake trout come to possess so many homoplasious behavioural traits? An intriguing study by Hamada et al. (1997) identified some genetic introgression between *Coregonus* species and the common ancestor of chum and pink salmon, so it might be possible that the convergent traits identified in our study were transferred by a historical interaction between lake trout and *Coregonus*. In general though, introgression is relatively rare within salmonines (McLennan 2007 and references therein), so we will focus our attention on other possible explanations for the occurrence of widespread homoplasy in the lake trout. These explanations are offered in an attempt to stimulate future studies on the historical biogeography and behavioural ecology of lake trout, and thus may be viewed as hypotheses subject to further testing.

The common ancestor of *Salvelinus* was probably a typical salmonine. Females migrated to streams and excavated and defended a series of nests in the gravel substrate in which to successively lay their eggs,

while males fought with one another to monopolize access to females and subsequent fertilizations. A population from that ancestral species (assuming *S. namaycush* is the basal member of the clade, but the scenario does not change if it is nested more deeply within *Salvelinus*) then either colonized (peripheral isolates speciation), or became isolated in (microvicariant speciation), a lake environment and some members of that peripheral population eventually began depositing eggs along lakeshores cleaned of debris by wind and wave action. Many factors may have influenced this transition from a nest-building to itinerant strategy. For example, selection on females for placing eggs in a self-cleaned depression (nest) may have been relaxed because silt was already being removed by waves and, as we note in this study, by the actions of fish swarming in shallow waters to spawn. These non-nesting females thus retained the plesiomorphic behaviour “progressively lay batches of eggs” but rather than depositing those batches in one or a series of defended nest sites, they now travelled extensively, distributing eggs across different areas favoured by wind and waves and free of silt (derived behaviour). Assuming that travelling is energetically cheaper than building a nest and defending a territory, which does not seem unreasonable given the intense nature of female–female aggressive interactions and digging behaviours (Crisp and Carling 1989; Barlaup et al. 1994), these non nesting females should show a net savings in their energy budget. The new itinerant spawning strategy may have been further favoured by selection if these fish were spawning in habitats that were unusually ephemeral; distributing clutches across many different locations decreased the probability that a random accident would destroy most or all of a female's reproductive output. To test these, and other factors that may have been involved in the switch from nest-building to an itinerant strategy, we need to compare sex ratios, density of spawning fish, habitat ephemerality, potential nest site locations, type and density of egg predators etc. between lake trout and their closest, nest-building relatives to highlight any unusual changes in lake trout that correlate with the shift in female behaviour (Brooks and McLennan 2002).

The new itinerant spawning strategy would have reduced intra-sexual selection favouring male–male competition (ancestrally around a territorial, nest-

building female) because such competition prevents males from staying close to the female at the moment of spawning if she is continuously moving. Studies on other salmonines have shown that fertilization efficiency is a function of the distance sperm must travel to the egg (e.g. Maekawa and Onozato 1986; Hutchings and Myers 1988; Mjølnerød et al. 1998). Since fertilization is extremely rapid following gamete release, the position of the male relative to the female becomes a paramount factor in paternity (Hoysak and Liley 2001; Liley et al. 2002). The focus of intra-sexual selection would thus be expected to shift from characteristics important in threat displays and fighting to characteristics that enhance a male's ability to maintain his position close to the traveling female (e.g., swimming efficiency, strength and endurance).

It is difficult to determine how the shift in the focus of intra-sexual selection has affected the strength of inter-sexual selection in lake trout. In many salmonine species, a female can exercise some choice by delaying nest preparation and spawning until a "preferred" male takes up the position closest to her (Schroder 1982; Foote 1989; Berejikian et al. 2000; de Gaudemar et al. 2000). Based on our observations, female lake trout do not appear to reject males, which might imply that inter-sexual selection has been relaxed in this species; an additional factor contributing to the loss of obvious sexual dimorphism. This observation, however, is limited to the range of our video equipment. We do not know how often the male closest to the female changes during the traveling phase, so it is possible that a female may use prolonged traveling as a more subtle way to assess the swimming abilities and endurance of her suitors. Swimming ability is a function of body size in swordtails, larger fish better able to hold their place in a current than smaller ones (Ryan 1988). This trait may thus convey information about male size, a focus of inter-sexual selection in many salmonines, to the traveling female. Endurance is intuitively linked to overall health, another fitness marker that may be important in a female's mate choice. If this dynamic is indeed occurring in lake trout, we predict that a female will go through numerous "drop-quiver-resume traveling" cycles before finally spawning because each drop to the ground allows her to familiarize herself with the males closest to her. She may then delay spawning

until one male accompanies her through more than one drop, thus demonstrating his swimming prowess, strength and stamina.

It is also difficult to untangle the factors that may have been responsible for the derived shift from day and night to strictly nocturnal spawning. Gunn (1995) suggested that the absence of both marked sexual dimorphism and male-male competition in lake trout was a consequence of this timing change. It is also possible, however, that the new itinerant female strategy, with its redirected focus on male strength and stamina rather than competition, favoured the loss of sexual dimorphism while the fish were still day spawners. Once again, we are faced with delineating a list of factors, such as the presence of visually biased egg predators, female attempts to escape male harassment etc. that might be responsible for the derived shift, but cannot favour any one over another or any combination, without additional comparative studies.

Summary

This study has presented some of the first detailed qualitative observations of complete lake trout spawning sequences. Clearly there is ample room for additional research concerning the evolution of the lake trout's breeding behaviour. For example, in order to begin collecting quantitative data, we need to study additional populations in which numerous cameras are set up, and individuals are marked for identification. Experimental and comparative studies are required to delineate the factors involved in the evolution of the novel female itinerant behaviour, as well as the shift from day and night to exclusively night spawning. Comparisons should be made between the lake trout and close relatives, as well as other salmonids in which nest-building behaviour has been lost [e.g., some populations of sockeye salmon (Wilson 1997) and arctic charr (Savvaitova 1969)] or does not occur (coregonines). Experimental studies are also required to examine the importance of inter-sexual selection in this system. Overall we hope that our study will help stimulate interest in the lake trout, to continue building the behavioral and life history database for this most enigmatic salmonine.

Acknowledgements Underwater recordings were taken with the help of Carmen Grisolia and Mafalda Esteve. This research was funded by an NSERC Operating Grant to DAM.

References

- Barlaup BT, Lura H, Saegrov H, Sundt RC (1994) Inter- and intra-specific variability in female salmonid spawning behaviour. *Can J Zool* 72:636–642
- Berejikian BA, Tezak EP, LaRae AL (2000) Female mate choice and spawning behaviour of Chinook salmon under experimental conditions. *J Fish Biol* 57:647–661
- Berst AH, Emery AR, Spangler GR (1981) Reproductive behaviour of hybrid charr (*Salvelinus fontinalis* × *S. namaycush*). *Can J Fish Aquat Sci* 38:432–440
- Brooks DR, McLennan DA (2002) The nature of diversity: an evolutionary voyage of discovery. University of Chicago Press, Chicago, Ill
- Crisp DT, Carling PA (1989) Observations on sitting, dimensions and structure of salmonid redds. *J Fish Biol* 34:119–134
- de Gaudemar B, Bonzom JM, Beall E (2000) Effects of courtship and relative mate size on sexual motivation in Atlantic salmon. *J Fish Biol* 57:502–515
- DeRoche SE (1969) Observations on the spawning habits and early life of lake trout. *Prog Fish-Cult* 31:109–113
- Esteve M (2005a) Spawning behaviour of the Salmoninae subfamily members: a phylogenetic study. Ph.D. dissertation. University of Barcelona. 202p
- Esteve M (2005b) Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. *Rev Fish Biol Fish* 15:1–21
- Esteve M, McLennan D (2007) The phylogeny of *Oncorhynchus* based on behavioral and life history characters. *Copeia* (in press)
- Fabricius E, Gustafson KJ (1954) Further aquarium observations of the charr *Salmo alpinus*. *Rep Inst Freshwater Res (Drottingholm)* 35:58–104
- Fabricius E, Lindroth A (1953) Experimental observations on the spawning behavior of whitefish, *Coregonus lavaretus* L., in the stream aquarium of the Holle Laboratory at River Indalsalven. *Rep Inst Freshwater Res (Drottingholm)* 35:105–112
- Footo CJ (1989) Female mate preference in Pacific salmon. *Anim Behav* 38:721–723
- Gunn JM (1995) Spawning behavior of lake trout: effects on colonization ability. *J Great Lakes Res* 21(Suppl 1):323–329
- Hamada M, Kido Y, Himberg M, Reist JD, Ying C, Hasegawa M, Okada N (1997) A newly isolated family of short interspersed repetitive elements (SINEs) in coregonid fishes (whitefish) with sequences that are almost identical to those of the SmaI family of repeats: possible evidence for the horizontal transfer of SINEs. *Genetics* 146:355–367
- Hawkins AD, Johnstone ADF (1978) The hearing of the Atlantic salmon, *Salmo salar*. *J Fish Biol* 13:655–673
- Holcik J, Hensel K, Nieslanik J, Skacel L (1988) The Eurasian Huchen, *Hucho Hucho*: largest salmon of the world. Dr. W. Junk Publishers, Dordrecht
- Hoysak DJ, Liley NR (2001) Fertilization dynamics in sockeye salmon and a comparison of sperm from alternative male phenotypes. *J Fish Biol* 58:1286–1300
- Hutchings JA, Myers RA (1988) Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*. *Oecologia* 75:169–174
- Liimatainen VA, Snucins EJ, Gunn JM (1987) Observations of lake trout (*Salvelinus namaycush*) spawning behaviour in low pH lakes near Sudbury, Ontario. Ontario Fisheries Acidification Report Series No. 87–10
- Liley NR, Tamkee P, Tsai R, Hoysak D (2002) Fertilization dynamics in rainbow trout (*Oncorhynchus mykiss*): effect of male age, social experience, and sperm concentration and motility on in vitro fertilization. *Can J Fish Aquat Sci* 59:144–152
- Maekawa K, Onozato H (1986) Reproductive tactics and fertilization success of mature male Miyabe char, *Salvelinus malma miyabei*. *Environ Biol Fish* 15:119–129
- Martin NV (1957) Reproduction of lake trout in Algonquin Park, Ontario. *Trans Am Fish Soc* 86:231–244
- Martin NV, Olver CH (1980) The lake charr, *Salvelinus namaycush*. In: Balon EK (ed) Charrs, salmonid fishes of the genus *Salvelinus*. Dr. W. Junk. Publ. The Hague, The Netherlands, pp. 205–277
- McLennan DA (2007) The sexual behavior of North American freshwater fish. In: Mayden R (ed) Systematics, historical ecology and North American freshwater fishes. Elsevier Science, New York (in press).
- Mjølnerød IB, Fleming IA, Refseth UH, Hindar K (1998) Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Can J Zool* 76:70–75
- Royce WF (1951) Breeding habits of lake trout in New York. *Fish Bull. US Fish and Wildlife Service* 59:59–76
- Ryan MJ (1988) Phenotype, genotype, swimming endurance, and sexual selection in a swordtail (*Xiphophorus nigrensis*). *Copeia* 1988:484–487
- Savvaitova KA (1969) Homologous variation in char species of the genera *Salvelinus* (Nilsson) and *Cristivomer* Gill and Jordan. *J Ichth* 9:18–34
- Schellart NAM, Popper AN (1992) Functional aspects of the evolution of the auditory system of Actinopterygian fish. In: Webster DB, Fay RR, Popper AN (eds) The evolutionary biology of hearing. Springer-Verlag, New York. pp 295–322
- Schroder SL (1982) The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. In: Brannon EL, Salo EO (eds) Salmon and trout migratory behavior symposium. University of Washington Press, Seattle, pp. 275–285
- Watson R (1999) Salmon, trout & char of the world: a fisherman's natural history. Swan Hill Press, England
- Wilson MF (1997) Variation in salmonid life histories: patterns and perspectives. Res Pap PNW-RP-498, US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR