

**This is an electronic reprint of the original article.
This reprint *may differ* from the original in pagination and typographic detail.**

Author(s): Syrjänen, Jukka; Sivonen, Kimmo; Sivonen, Olli

Title: Redd Counting for Monitoring Salmonids in Finnish Inland Waters

Year: 2014

Version:

Please cite the original version:

Syrjänen, J., Sivonen, K., & Sivonen, O. (2014). Redd Counting for Monitoring Salmonids in Finnish Inland Waters. In R. Carline, & C. LoSapio (Eds.), Looking back and moving forward. Proceedings of the Wild Trout XI symposium (pp. 288-294). Wild Trout Symposium. <http://www.wildtroutsymposium.com/proceedings-11.pdf>

All material supplied via JYX is protected by copyright and other intellectual property rights, and duplication or sale of all or part of any of the repository collections is not permitted, except that material may be duplicated by you for your research use or educational purposes in electronic or print form. You must obtain permission for any other use. Electronic or print copies may not be offered, whether for sale or otherwise to anyone who is not an authorised user.

REDD COUNTING IN MONITORING SALMONIDS IN FINNISH INLAND WATERS

Jukka T. Syrjänen¹, Kimmo Sivonen¹ and Olli Sivonen¹

¹Department of Biological and Environmental Science, University of Jyväskylä, PO Box 35, FI-40014 University of Jyväskylä, Finland. Phone: +358 505454615. Email: jukka.t.syrjanen@jyu.fi

Abstract

During recent years, systematic redd counting has been used as a monitoring method of wild Brown Trout *Salmo trutta* spawning stocks, both resident and lake-migrating, in the Lake District in Southern Finland. Counting is done by wading and viewing with an aqua-scope, and is related to channel microhabitat measurements, to estimation of gravel origin, to regression between redd length and female length, to regression between female length and egg number in redd, and to parr density. This produces valuable information about spawning environment, spawning stocks, and stock-recruitment ratio for management of stream-spawning fishes and river channels. Number of trout redds and of female spawners was mostly 10–30 (length of each stream sampled 200–500 m), and in maximum about 100 redds/individuals, per stream in Kymijoki watercourse. Average redd length was 1.71 m, water depth 57 cm, and water current velocity in three cm above bottom surface 27 cm/s. Most common dominant gravel size was 64–128 mm in pot and 32–64 mm in tail. Both natural and artificial gravel were important as spawning grounds, but gravel carried in with buckets by volunteers produced much more redds per gravel volume than gravel deposited with an excavator. Most often, redds were situated in small pools or holes inside riffle sections, but also in upstream edges of riffles in some larger rapids. About 70 % of redds were situated no more than 50 cm from a shelter, like a stone or a channel bank. In Kymijoki streams, mean fork length of female spawners was 38 cm, estimated from redd tail lengths. In other Finnish and Swedish spawning rivers of lake-migrating Brown Trout, average redd length was 2.5–3.0 m, and average female length 45–52 cm. In one Kymijoki stream, parr density was linearly correlated with egg density, estimated from redd number and redd tail lengths.

INTRODUCTION

Lake-migrating and sea-migrating Brown Trout *Salmo trutta* are classified as endangered and critically endangered, respectively, in Finland in the drainage area of the Baltic Sea (Rassi 2010). A century ago, landlocked Atlantic Salmon *Salmo salar* m. *Sebago* lived as wild in Vuoksi watercourse, the largest Finnish watercourse situated in the south-east, but now after being bred only in hatcheries for the past 42–45 years, the subspecies will possibly be returned into one of its three historical spawning streams in fall 2013. Main reasons for the weakness of wild trout stocks are strong fishing pressure on lakes (Syrjänen and Valkeajärvi 2010) and on the coastal Baltic Sea, mainly with gillnets, and stream damming. High fishing mortality will make it hard to restore the wild stock of landlocked Atlantic Salmon, too. On the other hand, stream channel restoration projects have been going on in Finland for the past 30 years, and restorations have been done mainly for fisheries. New artificial gravel beds have been usually created in channel restorations, but no information is available about the use of these beds by spawners.

In monitoring wild stocks of stream spawning salmonids, electrofishing of parr has been the most commonly used method. Horizontal echo sounding, fish counting on dams or in fishways, and rod catch have been used for Atlantic Salmon and migrating Brown Trout, too. In the Lake District in Southern Finland, stream channels are mainly short lake-outlet streams between lakes. There, redd counting has been used for monitoring of wild spawning stocks of Brown Trout in the 21st century. However, redd counting has been used for decades in some parts of Europe (e.g. Dauphin et al. 2010), and especially in North America (Beland 1996; Callagher et al. 2007).

A female Brown Trout usually makes one redd, sometimes two, when spawning, each redd including several nests or egg pockets (Klemetsen et al. 2003), and buries the eggs in gravel to depths of 1–20 cm. A redd consists of an upstream pot, which is a deeper hole compared to surrounding substratum, and a downstream tail or hump, where the female has piled gravel from the pot over the eggs (Fig 1.). In Finland, main spawning time is from mid-September to mid-October. Parr emerge from late May to late June. Thus, incubation time of eggs and alevins in bottom substrate is long, 7–9 months, depending on latitudinal location of the stream. To estimate spawning environment, redd structure, redd microhabitat factors, and female spawner length, 1,367 redds were sampled in six large watercourses in Finland and Sweden.

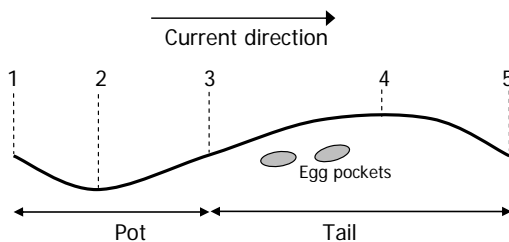


Figure 1. Side profile of the spawning redd of salmonids. Five example points are shown, where depth and current velocity can be measured. 1 = upstream edge of pot, 2 = deepest point in pot, 3 = border between pot and tail, 4 = highest point in tail, and 5 = downstream edge of tail.

METHODS

Study streams

Most of the trout redd data set was collected from streams of Kymijoki watercourse, situated in the Finnish Lake District, during years 2000–2012. Seven separate streams of five sub-watercourses were sampled: Arvaja (mean low flow 0.66, mean flow 2.0, and mean high flow 8.7 m³/s; flowing into Lake Päijänne), Rutajoki (0.35, 1.2 and 5.2 m³/s; Päijänne), Muuramenjoki (1.3, 3.3 and 11.1 m³/s; Päijänne), Rautalampi sub-watercourse (33, 45 and 92 m³/s; Konnevesi), Koivujoki (0.59, 2.2 and 7.6 m³/s; Pielavesi-Nilakka), Kärnä sub-watercourse (6.6, 15, and 32 m³/s; Keitele) and Läsänkoski (6.5, 15, and 25 m³/s; Puula). The seven streams include the most important spawning streams of trout in Kymijoki watercourse. Water quality is good or excellent in all streams and lakes, but bottom ice formation occurs in streams in some winters. Each lake has a surface area of 100–1,100 km², and has good or excellent Vendace *Coregonus albula* stocks as prey for lake-migrating trout. Each stream channel was dredged between the 1850s and the 1960s, but was restored in 1982–2011. However, restoration actions were usually slight, and channels were probably not returned to their natural construction. In restoration by environmental administration in 1997, 50–100 m³ of gravel deposited by excavator was added in the channel of Rutajoki. Then, in voluntary restoration in 2000, 10 m³ of gravel carried in with buckets by volunteers was added. In corresponding restoration actions In Koivujoki, 100–300 m³ of excavator gravel was added in 1994, and 10 m³ of bucket gravel in 2009. In these streams, excavator gravel was of smaller size and included both crushed rubble and filtered gravel, while bucket gravel was totally slightly larger filtered gravel. Some graveling volunteers carried out also the redd counting, remembering exact points of bucket gravel beds. Thus, excavator gravel and bucket gravel beds could be identified in the two streams. In Arvaja, 50–100 m³ of excavator gravel was added in 1996, and 5 m³ of bucket gravel in 2000's, but these two gravel classes could not be identified separately there. All data were collected after channel restoration and extra gravel restoration in each stream.

Additional trout redd data sets were collected from other watercourses from known spawning streams of lake-migrating Brown Trout. These were Heinävesi sub-watercourse flowing out from Lake Kermajärvi situated in Vuoksi watercourse in Southern Finland, rivers Oulanka and Kuusinki in Koutajoki watercourse in North-Eastern Finland flowing into Lake Pääjärvi in Russia, river Juutua in Paatsjoki watercourse flowing into Lake Inari in Northern Finland, rivers Hjoån and Hjällöbacken flowing into Lake Vättern in Southern Sweden, and rivers Gullspångsälven and Klaraälven flowing into Lake Vänern in Southern Sweden, in 2008–2012. Vänern tributaries were sampled before spawning time of landlocked Atlantic Salmon. Each lake has a surface area of 100–5,000 km². Water quality is excellent in all streams and lakes, and Vendace stocks are excellent in all lakes.

Redd sampling

Most of sampled riffle sections of a stream or whole rapids were waded through completely with aqua-scope from bank to bank to upstream direction. If it was not possible to sample the whole section, best spawning areas were sampled to find most of the redds in the section. In Kymijoki streams and sub-watercourses, size of sampling area was 0.3–2 ha in each stream and included 2–4 riffle sections per stream. Largest streams, Rautalampi, Heinävesi, Oulanka, Juutua and Klaraälven, were waded from bank to depth of 1–1.5 m. Clear, redd-shaped pits were classified as redds, but small and unclear-shaped pits were carefully dug out, so that 1–2 eggs were found, and the pit was identified as a redd. If no eggs were found despite of vigorous digging, the pit was abandoned and not measured. In Finnish streams, redd superimposition, i.e. several females spawned over each other's redds, was rare, as redds touched only occasionally each other. No more than of 2% of redd-shaped objects containing eggs could not be identified clearly as one redd or several redds. Thus, estimation of redd microhabitat factors was reliable in all Finnish streams, and estimation of the number of female spawners possible in Kymijoki sub-watercourses. In Vättern and Vänern inlets,

superimposition was more common, but microhabitat factors could be measured by rigorous sampling for each redd.

Total length and width of pot and tail were measured separately (Fig. 1). Most important microenvironmental factors, like water depth, current velocity 3 cm above substratum, and substratum particle size with modified Wentworth scale (Heggenes 1988) were measured, again separately for pot and tail. Distance from redd edge to a nearest possible shelter suitable for spawning fish was measured. Channel bank, woody debris with diameter of 10 cm or more, or a stone with the largest diameter of 40 cm or more and situated clearly above bottom level were classified as a shelter construction. The origin of redd gravel was classified into three categories: natural gravel, artificial gravel put in channels by excavator in restorations organized by environmental authorities (excavator gravel), and artificial gravel put in channel by volunteers with buckets (bucket gravel).

Estimation of female length and egg density

The fork length of a spawned female trout (L , cm) was estimated for each redd from the redd tail length (q , cm) as $\ln L = 0.60 \cdot \ln q + 0.86$ (modified from Crisp and Carling 1989). This produced length distribution of females. The egg number (E) buried by a female in her redd was calculated from female fork length (L , mm) as $E = 0.006266 \cdot L^{2.048}$ with regression of Elliott (1995). For egg density in a riffle section, egg number was summed from all redds and divided by the size of sampling area. In Rutajoki, the egg density was related annually to next fall density of age-0 parr in electrofishing during 12 years, and thus, a stock-recruitment curve was created for two riffle sections, Matkuksenkoski and Porraskoski. Length of both sections was 200 m, and they were separated by a 200-m long pool section.

Statistical analyses

Medians of total redd length, depth at the break of pot and tail, current velocity 3 cm above bottom substrate at the break of pot and tail, dominant particle size in tail, and estimated female length between lakes or (sub)watercourses were tested with nonparametric median test. In case of significant difference between medians, pairwise comparisons of medians were made. Water depth and current velocity were not tested for Vänern streams, as discharge was lowered substantially from autumnal normal by hydroelectric power plant to make redd counting possible in Gullspångälven. Current velocity was not measured for Inari stream. In Rutajoki, Spearman rank correlation was used on stock-recruitment data.

RESULTS

As main characteristics among the five Kymijoki sub-watercourses, averages of the minimum, mean and maximum values of total redd length (total $n = 991$) were 51, 171 and 429 cm, and of total (most often for tail) width 29, 79 and 238 cm, of water depth at border between pot and tail 19, 57 and 110 cm (total $n = 970$), and of current velocity 4, 27 and 75 cm/s (total $n = 421$). The most common dominant particle size groups were 64–128 mm and 32–64 mm just upstream from pot, 64–128 mm in pot and 32–64 mm in tail. Redds dug into natural substrate often included all sizes of particles of 1–200 mm. Sometimes, there were stones of 200–400 mm in tail, but this size of stones had not been moved during spawning. Average distance between the redd edge and the nearest shelter was 59 cm, and 70% of redds were situated no more than 50 cm from a shelter. Often, one edge of a redd touched a big stone, channel bank or woody debris. Averages of the minimum, mean and maximum values among the five Kymijoki sub-watercourses of female spawner length estimated from redd tail length (total $n = 991$) were 18, 38 and 72 cm.

Main result among five Kymijoki sub-watercourses and the five additional watercourses for total redd length was that length was larger in the five additional watercourses compared to the five Kymijoki sub-watercourses in all cases but one (median main test: $P < 0.001$, each pairwise test: $P < 0.05$, but in one case $P = 0.06$) (Table 1). In addition, median redd length was larger in Konnevesi outlet and Keitele inlet than in Päijänne inlets and Pielavesi-Nilakka inlet (each pairwise test: $P < 0.05$), and larger in Puula inlet than in Pielavesi-Nilakka inlet ($P < 0.001$). Median redd length did not differ among the five additional watercourses (each pairwise test: $P = 1.00$). Median depth was smaller in Vättern inlets than all other watercourses (median test: $P < 0.001$, each pairwise test: $P < 0.01$), and smaller in Pääjärvi, Päijänne (Kymijoki) and Pielavesi-Nilakka (Kymijoki) compared to Puula (Kymijoki), Keitele (Kymijoki), Konnevesi (Kymijoki), Inari and Kermajärvi (each pairwise test: $P < 0.001$). No differences were detected among eight watercourses for current velocity (median test: $P = 0.07$). Median of the most common particle size in redd tail was larger in Inari and Vänern than in other eight watercourses (median test: $P < 0.001$, each pairwise test: $P < 0.05$) (Table 1).

Table 1. Median and range of total length (cm), water depth (cm), current velocity (cm/s), and dominant particle size (mm) in tail of Brown Trout spawning redds, and female fork length (cm) in five Kymijoki sub-watercourses and five additional watercourses. Water depth and current velocity 3 cm above substratum were measured at point 3, at border between pot and tail (Fig. 1). N was minimum on current velocity and near maximum on all other factors. ND = no data.

Watercourse	N	Total length	Water depth	Current velocity	Dominant particle	Female length
Kymijoki						
Pielavesi-Nilakka	71–137	133 (60–420)	48 (15–95)	23 (2–102)	32–64 (8–256)	33 (18–79)
Konnevesi	8–179	170 (50–450)	80 (15–150)	21 (13–41)	32–64 (8–516)	37 (19–68)
Keitele	10–136	188 (70–460)	61 (22–100)	23 (12–78)	32–64 (16–128)	33 (18–71)
Päijänne	270–400	150 (35–450)	47 (13–117)	23 (2–105)	32–64 (8–256)	36 (16–72)
Puula	69–138	175 (55–450)	60 (24–101)	28 (2–63)	32–64 (2–128)	37 (18–77)
Additional watercourses						
Kermajärvi	17–96	230 (90–600)	86 (34–150)	22 (4–66)	32–64 (16–128)	45 (23–90)
Pääjärvi	67–76	245 (85–580)	43 (28–72)	32 (1–68)	32–64 (16–256)	45 (22–85)
Inari	30	300 (180–580)	82 (42–104)	ND	64–128 (32–256)	52 (35–77)
Vättern	41–101	265 (105–585)	35 (13–69)	23 (3–70)	32–64 (8–256)	50 (26–77)
Vänern	26–74	235 (100–590)	ND	ND	64–128 (16–516)	44 (25–92)

On a mesoscale, in smaller Kymijoki streams Rutajoki, Muuramenjoki, Arvaja and Koivujoki, 80–85% of redds ($n = 189$) were situated in riffles in downstream edges of holes or small pools, 10–15% in upstream edges of riffles, and less than 10 % in downstream glides of riffles. On larger Kymijoki streams, 80–83 % of redds ($n = 317$) were situated in riffles, and 17–20% in upstream edges of riffles. Only riffle sections sampled thoroughly were included here. However, largest excavator gravel beds were always observed in upstream edges of riffles, and these beds were often situated in low current areas without shelter nearby, and some of beds were grown over with macrophytes.

In Rutajoki in 2000–2003, 40 % of all redds (total $n = 72$) were situated in natural gravel, 26% in excavator gravel, and 33 % in bucket gravel. In 2004–2007, corresponding proportions were 22, 47

and 31 % (total $n = 54$), and in 2008–2011, proportions were 44, 45 and 11 % (total $n = 64$). Bucket gravel beds created by volunteers were small, and spring floods and trout redd digging most likely moved gravel downstream. Gradually, bucket gravel beds disappeared, so that 10–20% of beds was left in fall 2011. Almost all excavator gravel beds, which were much larger, persisted to fall 2011. In Koivujoki in 2009–2012, 38% of redds were in natural gravel, 19 % excavator gravel, and 35% in bucket gravel. Still, 80–90% of bucket gravel beds were left in fall 2012. In Arvaja in 2007–2012, 42% of redds were situated in natural gravel and 58% in restoration gravel.

In Kymijoki watercourse, number of redds, and thus the number of female spawners, was mostly 10–30 redds or individuals per stream, and in maximum about 100 redds or individuals in Rautalampi sub-watercourse, and mostly 5–15 redds or individuals per a riffle section. In some cases, no redds were found in a riffle section. Median female length was smaller in Pielavesi-Nilakka (Kymijoki) than in other nine watercourses (median test: $P < 0.001$ and each pairwise test: $P < 0.05$). Median length was smaller in Konnevesi (Kymijoki) and Päijänne (Kymijoki) compared to all five additional watercourses (each pairwise test: $P \leq 0.001$), and smaller in Keitele (Kymijoki) and Puula (Kymijoki) compared to Kermajärvi, Pääjärvi, Inari and Vättern (each pairwise test: $P < 0.05$) (Table 1).

In Rutajoki, egg density was 0–13 eggs/m² in Matkuksenkoski and 1–8 eggs/m² in Porraskoski between years. Density of age-0 parr was positively correlated to egg density of previous fall in both sites, *Spearman's rho* = 0.82 ($P = 0.001$) and 0.66 ($P = 0.02$), respectively.

DISCUSSION

Redd counting by wading could well be a reasonable method in surveying and monitoring spawning stocks or stream-spawning fish. The method is sufficiently easy and cheap to be used especially in small streams or short riffle sections. However, the estimated number of redds and the size of female spawning stock is a minimum estimation, if real redds are identified by finding eggs. Some proportion of redds, especially of small ones less than one meter long and redds situated in deep water, is likely not to be found in counting. More, only experienced redd counter personnel can give reliable estimations about the number of redds. In two streams in Idaho, different counters gave redd number estimations of 28–254 % of the numbers estimated by experts of the streams, but counters were not allowed to search eggs to verify deposition. (Dunham et al. 2001).

Spawning depth of Brown Trout varies considerably in published records. In three regulated Norwegian rivers with mean flow of 18–105 m³/s and seasonal flow highly fluctuating, average depth of redds was 90–137 cm, but sampling was done by diving (Wollebæk et al. 2008). On the contrary, Louhi et al. (2008) reported the most common depth of 20 cm and common range of 15–45 cm in their review of 17 published reports of spawning microhabitats of the species, but sampled rivers were mainly small and located more south than North Europe. Average depth in Kymijoki watercourse, 57 cm, was between these. In our data, smallest median, 35 cm, was in the smallest and southernmost streams, Vättern inlets. Highest medians, 80–86 cm, were detected in largest streams, and are most probably underestimations, as deepest areas could not be sampled by wading. In Nordic Countries, trout might be adapted to spawn relatively deep if possible, because of long incubation time of eggs and alevins, and thus of higher risk of eggs or alevins to face drought during long periods of low temperatures and low flows. On the other hand, current velocity was similar, 29 cm/s, in Wollebæk's et al. (2008) work measured 5 cm above bottom substrate in front of the redd, compared to our medians of 21–32 cm/s. Louhi et. al (2008) reported most common velocity of 40 cm/s, but did not give the measurement depth used. In our data, most common

dominant particle size was slightly larger, 32–64 mm, than in Louhi's et. al (2008) review, 16–64 mm.

Environmental authorities preferred to deposit gravel mainly in upstream edges of riffles without shelter sites in their channel restoration actions during previous decades in Finland, but trout preferred to spawn mainly inside riffle sections very near stones, woody debris, or channel bank. Bucket gravel carried by expert volunteers produced clearly more redds than excavator gravel compared by gravel volume, but bucket graveling should be repeated each decade to maintain the small artificial gravel beds.

Redd length range was large, 51–429 cm, in Kymijoki watercourse, indicating wide range in female length. Because sub-watercourse medians were all less than 200 cm, small redds dominated in the sample. Redds in additional watercourses with migratory spawners were longer on average, and the length difference cannot be explained with microhabitat factors, as no differences were detected in current velocity among sites and only few differences in redd particle size. In the three Norwegian rivers, where spawning stocks were mainly lake-migrating, partly resident, mean length of redds was 192–236 cm (Wollebæk et al. 2008), falling between Kymijoki watercourse and the additional watercourses in our data. Most probable explanation for dominance of small redds in Kymijoki watercourse is the small size of female spawners, which in turn indicate that spawning stocks consist mainly of resident spawners, and lake-migrating larger females are few. Number of female spawners is probably low compared to environmental capacity, as redds were usually of low number in Kymijoki streams. Egg density estimations by redd counts seem reliable, because parr density was strongly correlated to egg density in Rutajoki. Thus, size of spawning stock controls parr abundance, at least in this stream.

Yet, absolute length values of females estimated from redd tail lengths should be used with caution, and reliability of length distributions estimated from redds should be tested by comparing it to distributions in rod catch, in trap catch for hatcheries, or in fish counter device in fishways. However in the 1910s, mean total length of female spawners caught for hatcheries in streams of Keitele and Puula sub-watercourses was 69 cm, females of 65–75 cm were abundant in catches, and no females less than 56 cm existed in samples (Järvi 1936). Largest observed individuals were 10–15 kg in Kymijoki watercourse at that time (Syrjänen and Valkeajärvi 2010). Although sampling methods between Järvi's (1936) work and this work are different, we believe that size and probably number of female spawners have collapsed in a century in Kymijoki watercourse, and the main reason for this is previous and current high fishing mortality on lakes because of almost unregulated fishing, and previous high fishing mortality also on streams during 20th century (Syrjänen and Valkeajärvi 2010). In Kymijoki watercourse, total number of female spawners per a lake is now some tens or up to some hundreds, but not more, and number of lake-migrating larger females is probably much less. In Vuoksi watercourse, condition of migratory spawning stock is not better as a whole, as Kermajärvi outlet is almost the only area left in the watercourse, where migratory trout spawn naturally.

ACKNOWLEDGEMENTS

This work was funded by the Ministry of agriculture and forestry, Maj ja Tor Nessling Foundation, Häme Regional Fund of the Finnish Cultural Foundation, Finnish Game and Fisheries Research Institute, and ELY-centres of Central Finland, South Savonia and North Savonia. Konnevesi Fisheries Society supported small monitoring projects. Vesi-Visio Co-operative carried out remarkable part of field sampling, and students and trainees of University of Jyväskylä gave substantial help on field. In Sweden, Vätternvårdsförbundet and Karlstad University supported field sampling.

REFERENCES

- Beland, K. F. 1996. The relation between redd counts and Atlantic salmon (*Salmo salar*) parr populations in Dennys River, Maine. *Canadian Journal of Fisheries and Aquatic Sciences* 53:513–519.
- Callagher, S. P., P. K. J. Hahn, and D. H. Johnson. 2007. Redd counts. Pages 197–231 in D. H. Johnson, B. M. Shrier, J. S. O’Neal, J. A. Knutzen, X. Augerot, T. A. O’Neal, and T. N. Pearsons, editors. *Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations*. American Fisheries Society. Bethesda, Maryland. 478 p.
- Crisp, D. T., and P. A. Carling. 1989. Observations on siting, dimensions and structure of salmonids redds. *Journal of Fish Biology* 34:119–134.
- Dauphin, G., E. Prévost, C. E. Adams, and P. Boylan. 2010. Using redd counts to estimate salmonid spawner abundances: A Bayesian modeling approach. *Fisheries Research* 106(1):32–40.
- Dunham, J., B. Rieman, and K. Davis. 2001. Sources and magnitude of sampling error in redd counts for bull trout. *North American Journal of Fisheries Management* 21:343–352.
- Elliott, J. M. 1995. Fecundity and egg density in the redd for sea trout. *Journal of Fish Biology* 47:893–901.
- Heggenes, J. 1988. Effect of experimentally increased intraspecific competition on sedentary adult brown trout (*Salmo trutta*) movement and stream habitat choice. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1163–1172.
- Järvi, T. H. 1936. Yhtä ja toista Huopanan ja Keiteleen järvilohista. *Suomen Kalastuslehti* 43:200–206. In Finnish.
- Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O’Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12:1–59.
- Louhi, P., A. Mäki-Petäys, and J. Erkinaro. 2008. Spawning habitat of Atlantic salmon and brown trout: general criteria and intragravel factors. *River Research and Applications* 24:330–339.
- Rassi, P., E. Hyvärinen, A. Juslén, and I. Mannerkoski. 2010. The 2010 Red List of Finnish Species. *Ympäristöministeriö & Suomen ympäristökeskus, Helsinki*. 685 p.
- Syrjänen, J., and P. Valkeajärvi. 2010. Gillnet fishing drives lake-migrating brown trout to near extinction in the lake Päijänne region, Finland. *Fisheries Management and Ecology* 17(2):199–208.
- Wollebæk, J., R. Thue, and J. Heggenes. 2008. Redd site microhabitat utilization and quantitative models for wild large brown trout in three contrasting boreal rivers. *North American Journal of Fisheries Management* 28:1249–1258.