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Influence of European sculpin (*Cottus gobio*) on Atlantic salmon (*Salmo salar*) recruitment and the effect of gravel size on egg predation: Implications for spawning habitat restoration

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Influence of European sculpin, *Cottus gobio*, on Atlantic salmon *Salmo salar*, recruitment and the effect of gravel size on egg predation -implications for spawning habitat restoration

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Running title: influence of European sculpin on Atlantic salmon

Abstract the study examined if recruitment of juvenile Atlantic salmon, *Salmo salar* L., was influenced by the presence of European sculpin, *Cottus gobio* L., and if the spawning substrate size used by salmon influence sculpin predation on salmon eggs. A combination of information on spawning site selection by female salmon and associated densities of juvenile salmon indicated that recruitment of juvenile salmon was ten times lower in areas where sculpin was present than areas without sculpin. Predation rate on salmon eggs was found to be dependent on substrate size in artificial redds created in stream aquaria using four different sizes of substrate (13, 23, 37 and 62 mm). Predation rate averaged 83% in the aquaria with the largest substrate size, whereas a rate of only 2-3% was observed using smaller substrate sizes. Sculpin may thus be an important factor influencing the recruitment of juvenile salmon. Selecting small enough gravel sizes during restoration of salmon spawning habitat could therefore be important to minimize egg predation.

KEYWORDS: competition, predation, restoration.

Introduction

In North America, five species of sculpin, *Cottus cognatus* (Richardson), *Cottus hypselurus* (Robins & Robinson), *Cottus aleuticus* (Gilbert), *Cottus bairdi* (Girard), *Cottus asper* (Richardson) have been shown, both in laboratory and field studies, to be important predators on egg and fry of several salmonid species (Savino & Henry 1991; Miller *et al.* 1992; Berejikian 1995; Hudson *et al.* 1995; Biga *et al.* 1998; Foote & Brown 1998; Chotkowski & Marsden 1999; Fitzsimons *et al.* 2002; Tabor *et al.* 2004). By contrast, the effect of sculpin predation on salmonids in Europe appears to differ. Several studies found interactions between one of the most common European sculpin species, *Cottus gobio* L., and salmonids, but as a result of habitat and diet overlap and not predation (Pihlaja *et al.* 1998; Jørgensen *et al.* 1999; Gabler *et al.* 2001; Elliott 2006). However, field observations of *C. gobio* in interstitial spaces of spawning redds of brown trout, *Salmo trutta* L., together with experimental studies where *C. gobio* has been shown to predate on brown trout, *Salmo trutta* L., fry (Gaudin & Heland 1984; Gaudin 1985; Bardonet & Heland 1994; Gaudin & Caillere 2000) suggest that their impact on salmonid recruitment through predation is unclear.

Several restoration programmes have recently been initiated in northern Sweden (Nilsson *et al.* 2005). These actions often include addition of spawning substrate into rivers and streams to improve salmon reproduction and recruitment. Selection of spawning substrate for habitat enhancement, however, needs to ensure high egg survival. Most studies on the effect of substrate size on egg and alevin survival have focused on water circulation, oxygen concentration and sediment accumulation. The general conclusion is that coarse substrate promotes higher water circulation, higher oxygen concentrations and low accumulation of sediments resulting in higher survival of eggs and embryos (Witzel & MacCrimmon 1983; Olsson & Persson 1986; Olsson &

Persson 1988; Bennett *et al.* 2003; Lapointe *et al.* 2004). The effect of spawning substrate on egg predation has received much less attention. In Lake Michigan, Biga *et al.* (1998) found that the ability of mottled sculpin, *Cottus bairdi* (Girard), to predate on rainbow trout, *Oncorhynchus mykiss* (Walbaum), eggs placed in rock piles was directly related to substrate size. They found that large substrate with larger interstitial spaces allowed greater access to *C. bairdi* to successfully penetrate the rock piles. Two sizes of substrate were tested, 5-10 and 10-22 cm in diameter. Egg predation occurred in both substrate sizes but was substantially higher in the larger size class. It is reasonable to assume that substrate size-dependent egg predation may also apply to Scandinavian rivers and is therefore relevant to the selection of substrate used for restoration works. *Cottus gobio* is smaller than the *C. bairdi* and is therefore more likely to be able to access egg pockets buried in smaller substrate sizes, such as are used by Atlantic salmon for spawning (0.7-13 cm) (Armstrong *et al.* 2003).

The purpose of the study was to investigate if recruitment of juvenile Atlantic salmon was reduced in the presence of *C. gobio* within the river and to assess if *C. gobio* predate on salmon eggs, and if so, how predation is affected by the size of the spawning substrate.

Material and methods

Study site

River Vindelälven originates in the Scandinavian mountains and flows in a south-easterly direction for about 400 km to join the River Umeälven approximately 42 km upstream from the outlet in the Bothnian Bay (63°50´N, 20° 05´E) (Fig. 1). River Vindelälven has a snow-dominated flow regime with a maximum flow of 1000 $m^3 \cdot s^{-1}$ during snowmelt in June. Average annual discharge is 180 $m^3 \cdot s^{-1}$ with a minimum winter discharge of 40 $m^3 \cdot s^{-1}$. Ice covers the river from

November to April. The fish fauna is dominated by Atlantic salmon, brown trout, northern pike, *Esox lucius* L., Eurasian minnow, *Phoxinus phoxinus* (L.), burbot, *Lota lota* (L.), Eurasian perch, *Perca fluviatilis* (L.) and European grayling *Thymallus thymallus* L., all of which occur throughout the whole system. *Cottus gobio*, which is also a common species in the river, is only found in the lower 200 km of its course. Salmon reproduction occurs in late October along the lower 250 km of the river (Swedish Electrofishing Register - SERS). This situation provides an opportunity to evaluate differences in salmon recruitment between areas with and without *C. gobio* within the same river. The riparian surroundings consist of managed boreal coniferous forest predominated by Scots pine, *Pinus sylvestris* (L.) and Norway spruce, *Picea abies* (L.).

Salmon spawning locations

A total of 190 female salmon were tagged with radio transmitters during their upstream spawning migration between 1997 and 1999 and returned to the river (see Östergren [2007] for details). The salmon tagging was conducted from July to September at a fish ladder located close to the outlet the River Umeälven into the Bothnian Bay (Fig. 1). All salmon ascending the ladder were captured and identified to sex before being released. The total number of ascending females was 1282, 265 and 1434 in 1997, 1998 and 1999, respectively. All these fish migrate up the River Vindelälven because the River Umeälven is dammed for hydroelectric power generation and there is no possibility for fish passage. Upstream migration of each radio-tagged individual was tracked twice weekly by a combination of airplane, car and foot and the location at spawning time was identified. In 1997, 1998 and 1999 spawning position data were obtained from 40, 34 and 51 females representing 4, 15 and 2 % of the total ascending female populations.

Fishery surveys

Twenty three fixed electric fishing locations were established along the lower 250 km of the river, 12 sites within and 11 sites outside the area with *C. gobio*. All electric fishing sites extended out from the bank to approximately knee-deep water, i.e. depth was approximately the same among all sites and ranged from 20-50 cm. Electric fishing was conducted by two crew members with one dip net in August 1998 through 2000 using one removal. Population density estimates of age 0+ salmon and *C. gobio* were calculated following Bohlin *et al.* (1989). Catchability estimates (P) were obtained from SERS; age 0+ salmon $P = 0.45$ and *C. gobio* $P = 0.3$. All fish caught were identified to species and measured to the nearest mm and released. Salmon ≤ 70 mm were considered to belong to the 0+ age class.

During electric fishing the dominant water velocity and substrate size were visually classified into one of three water velocity and nine substrate size categories. Water velocity categories 1, 2 and 3 represent 0-0.2, 0.2-0.7 and >0.7 $m \cdot s^{-1}$. Substrate size categories 1-9 represent <0.02, 0.02–0.2, 0.2–2, 2–10, 10–20, 20–30, 30–40, 40–200 cm in diameter plus bedrock.

Juvenile salmon recruitment

At the time of salmon spawning in late October all radio-tagged salmon located within one km upstream or downstream of each electric fishing site were counted. The positions of radio-tagged salmon were assumed to be representative of the total spawning female population (Thorstad *et al.* 2000). The length of the zone in which spawning females were counted, 1 km downstream and upstream of each electrofishing site, was used because 1-2 km is close to the maximal distance juvenile Atlantic salmon have been observed to disperse during the first summer (Beall *et al.* 1994; Webb *et al.* 2001). All females spawning within this zone were therefore assumed to contribute to the local density of age 0+ salmon the following summer.

By computing the percentage of the radio-tagged salmon located at each electrofishing site, the total number of female salmon within that same area was estimated. By combining the number of female salmon located at each electrofishing site during spawning time, and the density of age 0+ salmon the following year, a recruitment index (no. of age 0+ ind.•$100m^{-2}$•spawning $female^{-1}$) could be calculated for each electrofishing site.

Substrate and egg predation

The experimental study was conducted at the Umeå Marine Research Station (UMF) (63° 47´N, 20° 17´E) in Northern Sweden (Fig. 1). Twenty stream aquaria, 1.4 m long, 0.4 m wide and 0.5 m deep were used (Fig. 2). Water was continuously supplied at a flow rate of 10 L•min^{-1} and the depth was maintained at 30 cm. Constant water velocity was provided by a propeller located at one end of each stream aquarium. Water velocities ranged between 10-15 cm•s^{-1} and were equal between aquaria. Water temperature in the aquaria was maintained at 1 °C to mimic the range observed in northern Swedish rivers during most of the natural egg incubation period between November and April.

One artificial spawning redd was constructed by placing 20 L of gravel in a pile in the centre of each aquarium (Fig. 2). Four different sizes of gravel were used with a mean diameter of 13 ± 3, 23 ± 4, 37 ± 6 and 62 ± 10 mm (mean ± standard deviation), respectively, representing medium to very coarse gravel (Gordon *et al.* 1992). This range of sizes is near the mid to lower range of substrate size used by Atlantic salmon (0.7-13 cm) (Armstrong *et al.* 2003). Each substrate size was replicated in five separate stream aquaria. Fifty eyed Atlantic salmon eggs, from the wild river Vindelälven stock, were inserted into the bottom of each artificial spawning redd using a pipe (Fig. 2).

To simulate the natural size distribution of *C. gobio* populations, one wild captured adult, 8.6 ± 1.9 g (mean ± S.D.), and one juvenile *C. gobio*, 4.1 ± 1.8 g, were added to each aquarium. Chironomids larvae, which constitute natural *C. gobio* prey (Englund 2005), were delivered every third day at a rate 2 % of the total *C. gobio* body weight in each aquarium to serve as an alternative food resource.

After 15 days, the *C. gobio* were recaptured and the number of eggs remaining was determined. Growth, Daily growth coefficients (DGC), of *C. gobio* were calculated following Cowley (1992), DGC = 100 ($m_2^{0.333}$-$m_1^{0.333}$) t^{-1}, where m_2 and m_1 are the weights at the end and start of the study, respectively, and t is the number of days between measurements.

Analyses

Salmon recruitment (no. of age 0+ ind.•100m^{-2}•spawning female^{-1}) was compared between areas of the River Vindelälven with and without *C. gobio* using Analysis of Variance (ANOVA). Data were log transformed to meet the assumption of parametric analyses. Linear regression was used to explore the relationship between salmon recruitment and *C. gobio* density. In the laboratory study, differences in egg predation rates, fraction eaten (%), (arcsine $\sqrt{x}$ transformed) and total growth of *C. gobio* between aquaria with redds of different substrate sizes were calculated using ANOVA, followed by Tukey's *post-hoc* tests to determine which groups differed from each other. All statistical analyses were performed using Minitab v14.

Results

Salmon recruitment

The number of radio-tagged female salmon located within 1 km upstream or downstream of electric fishing sites at spawning time ranged from 1 and 7 individuals. Water velocity and substrate size did not vary between electric fishing sites located within and outside the area where *C. gobio* occurred. Overall, water velocity and substrate size categories tended to be within the classes that represent 0-0.2 m•s^{-1} and 30–40, 40–200 cm in diameter and bedrock (Fig. 3).

Densities of age 0+ salmon estimated by electric fishing ranged between 0 and 91.9 ind.•100m^{-2}. The mean density of salmon in the river sections without *C. gobio* was 11.2 ± 3.7 (mean ± standard error) ind.•100m^{-2} whereas salmon density in the sections with In the river section without *C. gobio* was 1.1 ± 0.3. The mean density of In the river section without *C. gobio* was 17.3 ± 2.6 with a range of 1.4-73.7 ind.•100m^{-2}. The mean density ratio between In the river section without *C. gobio* and age 0+ salmon was 18:1, range 0.8:1–73:1.

Recruitment (no. of age 0+ ind.•100m^{-2}•spawning female^{-1}) differed significantly between areas (ANOVA, d.f. =1, $F = 4.74$, $P = 0.041$) with no variation between years (d.f. = 2, $F = 0.21$, $P = 0.812$). Mean, three-year average (1998-2000), recruitment was 0.41 ± 0.17 (mean ± S.E.), in the section without *C. gobio* compared with 0.04 ± 0.02 in the section with *C. gobio*. No significant correlation between *C. gobio* density and salmon recruitment was found in the section with *C. gobio* (d.f. =1, $F = 3.27$, $P = 0.104$, $r^2 = 0.27$).

Egg predation

Fifteen days after sculpin were introduced, 0-44 out of the 50 salmon eggs placed in each aquarium were consumed, representing a predation rate of 0-88 %. A total of 1.0 ± 0.5, 0.8 ± 0.6, 1.4 ± 0.7, 41.4 ± 3.0 (mean ± SE) eggs were consumed for the substrate size classes 13, 23, 37 and 62 mm respectively. Predation rate on eggs differed significantly (ANOVA, d.f. = 3, $F = 15.50$, $P < 0.000$) among substrate sizes 82.8 ± 5.9 % (mean ± standard error) for substrate size 62.1

mm, and 1.6 - 2.8 % (range) for the remaining sizes (Fig. 4). There were no differences in egg predation among substrate sizes 13, 23, and 37 mm but it was significantly higher for the 62 mm substrate size (Tukey *post-hoc* test).

Mean total *C. gobio* growth was significantly higher (ANOVA, d.f. = 3, $F = 20.72$, $P < 0.001$) in aquaria with substrate size 62.1 mm than aquaria with smaller substrate sizes (Tukey *post-hoc* test; Fig. 4). There were no differences in growth between the other substrate sizes.

Discussion

Recruitment of juvenile salmon in the River Vindelälven was negatively affected by the presence of *C. gobio*. The mean recruitment index was 0.41 in the absence of *C. gobio* compared with 0.04 in its presence. Furthermore, the stream aquaria experiment showed that egg predation by *C. gobio* can be substantial and that the size of the spawning substrate influences predation rate. Several other studies have also concluded that freshwater sculpins are an important egg predator and may be a regulatory factor on salmonines (Savino & Henry 1991; Miller *et al.* 1992; Berejikian 1995; Hudson *et al.* 1995; Biga *et al.* 1998; Foote & Brown 1998; Chotkowski & Marsden 1999; Fitzsimons *et al.* 2002; Tabor *et al.* 2004).

However, these results contradict Pihlaja *et al.* (1998) who found no effect of *C. gobio* on Atlantic salmon juvenile densities in northern Finland. One reason for this difference might be that the density of juvenile Atlantic salmon was not adjusted by the spawning activity within different stream sections. Spatial differences in spawning activity can cause large variation in juvenile density, which can confound an assessment of the importance of other species or environmental factors, i.e. low densities of parr would imply either low recruitment or low spawning activity. Elliott (2006) studied the interactions between *C. gobio* and brown trout during over a 34-year period and found no negative effects of *C. gobio* even when adjusting brown trout densities for spawning activity. However, his studies were in a system dominated by gravel (Elliott 2004), and gravel is defined as particle sizes between 5.6 and 16 mm (Gordon *et al.* 1992), which, based on the findings of the present study, would reduce the possibilities of egg predation. Another explanation for the findings from the River Vindelälven could be the high *C. gobio* to juvenile Atlantic salmon ratio with a maximum of 73:1. Pihlaja *et al.* (1998), study on the River Teno was during the early colonisation phase of *C. gobio* following its accidental introduction in 1979. As a result, the *C. gobio* to Atlantic salmon density ratio was much lower, maximum 4:1. In rivers where the *C. gobio* to Atlantic salmon ratio is low the effects are probably less pronounced than in high ratio systems.

The lack of a relationship between salmon recruitment and *C. gobio* density could be the result of low accuracy of *C. gobio* population density estimates. Species that exhibit low electric fishing catchability (P), i.e. *C. gobio* $P = 0.17$-0.34 (Utzinger *et al.* 1998), generate low precision in population density estimates (Bohlin *et al.* 1989).

The results suggested that salmonid eggs are a valuable food resource for *C. gobio* growth during low temperature periods when other food items are scarce. However in the experimental study the substrate sizes used may not fully reflect the composition of natural spawning redds of Atlantic salmon (Kondolf *et al.* 1993; Kondolf 2000). Variation of substrate sizes in spawning redds naturally regulates access of bentic predators; with a higher proportion of substrate sizes below some threshold value lowering predator access (Biga *et al.* 1998).

Substrate used in spawning habitat restoration projects often originate from commercial gravel workings, which only supply sorted homogenous fractions. Fisheries managers aiming to enhance or conserve salmonid populations through addition of spawning substrate should identify which potential egg predators are present in their system and which substrate sizes limit their ability to access spawning redds. The best results might be achieved if substrate is chosen that both maximises embryo survival, but minimise egg predation. Olsson & Persson (1986) demonstrated that maximal (95 %) egg-to-fry survival of brown trout was obtained at substrate diameters of 18 mm. According to the present study, a substrate diameter of ≤ 37 mm would be sufficient to prevent egg predation by *C. gobio*. and large enough to ensure high survival.

Future research will need to shed more light on the complex interactions between bentic predators, spawning substrate, embryo survival and salmonid populations. Such studies will have important implications for habitat management, particularly during restoration projects.

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References

Armstrong J.D., Kemp P.S., Kennedy G.J.A., Ladle M. & Milner N.J. (2003) Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62,** 143-170.

Bardonnet A. & Heland M. (1994) The influence of potential predators on the habitat preferenda of emerging brown trout. *Journal of Fish Biology* **45,** 131-142.

Beall E., Dumas D., Claireaux L. & Marty C. (1994) Dispersal patterns and survival of Atlantic salmon (*Salmo salar*) juveniles in a nursery stream. *ICES Journal of Marine Science* **51,** 1-9.

Bennett D.H., Connor W.P. & Eaton C.A. (2003) Substrate composition and emergence success of fall chinook salmon in the Snake River. *Northwest Science* **77,** 93-99.

Berejikian B.A. (1995) The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Orcorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 2476-2482.

Biga H., Janssen J. & Marsden J.E. (1998) Effects of substrate size on lake trout egg predation by mottled sculpin. *Journal of Great Lakes Research* **24,** 464-473.

Bohlin T., Hamrin S., Heggeberget T.G., Rasmussen G. & Saltveit S.J. (1989) Electrofishing – Theory and practice with special emphasis on salmonids. *Hydrobiologia* **173:** 9-43.

Chotkowski M.A. & Marsden J.E. (1999) Round goby and mottled sculpin predation on lake trout eggs and fry: Field predictions from laboratory experiments. *Journal of Great Lakes Research* **25,** 26-35.

Cowley C.D. (1992) Nutrition: estimating requirements of rainbow trout. *Aquaculture* **100,** 177-189.

Elliott J.M. (2004) *Quantitative Ecology of the Brown Trout*. Oxford: Oxford University Press, 286 pp.

Elliott J.M. (2006) Periodic habitat loss alters the competitive coexistence between brown trout and sculpins in a small stream over 34 years. *Journal of Animal Ecology* **75,** 54-63.

Englund G. (2005) Scale dependent effects of predatory fish on stream benthos. *Oikos* **111,** 19-30.

Foote C.J. & Brown G.S. (1998) Ecological relationship between freshwater sculpins (genus Cottus) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1524-1533.

Fitzsimons J.D., Perkins D.L. & Krueger C.C. (2002) Sculpins and crayfish in lake trout spawning areas in Lake Ontario: Estimates of abundance and egg predation on lake trout eggs. *Journal of Great Lakes Research* **28,** 421-436.

Gabler H.M., Amundsen P.A. & Herfindal T. (2001) Diet segregation between introduced sculpin (*Cottus gobio* L.) and Atlantic salmon parr (*Salmo salar* L.) in a sub-Arctic river. *Archiv fur Hydrobiologie* **151,** 609-625.

Gaudin P. (1985) Predation by the sculpin (*Cottus gobio* L.) on brown trout fry (*Salmo trutta* L.): Total length of prey and predator. *Hydrobiologia* **122,** 267-270.

Gaudin P. & Heland M. (1984) Influence of sculpin adults (*Cottus gobio* L.) on brown trout (*Salmo trutta* L.) fry: Experimental study in semi-natural environments. *Acta Oecologia* **5,** 71-83.

Gaudin P. & Caillere, L. (2000) Experimental study of the influence of presence and predation by sculpin, *Cottus gobio* L., on the drift of emergent brown trout, *Salmo trutta* L. *Archiv fur Hydrobiologie* **147,** 257-271.

Gordon N.D., McMahon T.A. & Finlayson B.L. (1992) *Stream Hydrology. An Introduction for Ecologists*. Chichester: Wiley, 429 pp.

Hudson P.L., Savino J.F. & Bronte C.R. (1995) Predator-prey relations and competition for food between age-0 and slimy sculpins in the Apostel Island region of Lake Superior. *Journal of Great Lakes Research* **21,** 45-457.

Jørgensen L., Amundsen P.A., Gabler H.M., Halvorsen M., Erkinaro J. & Niemelä E. (1999) Spatial distribution of Atlantic salmon parr (*Salmo salar* L.) and sculpin (*Cottus gobio*

L.) in lotic and lentic habitats of a diversified watercourse in northern Fennoscandia. *Fisheries Research* **41,** 201-211.

Kondolf G.M., Sale M.J. & Wolman M.G. (1993) Modification of fluvial gravel size by spawning salmonids. *Water Recourse Research* **29,** 2265-2274.

Kondolf G.M. (2000) Assessing salmonid spawning gravel quality. *Transactions of the American Fisheries Society* **129,** 262-281.

Lapointe M., Bergeron N., Berube F., Pouliot M. & Johnston P. (2004) Interactive effects of substrate sand and silt contents on redd-scale hydraulic gradients and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 2271-2277.

Miller J.E., Savino J.F. & Neely R.K. (1992) Competition for food between crayfish (*Orconectes virilis*) and the slimy sculpin (*Cottus cognatus*). *Journal of Freshwater Ecology* **7,** 127-136.

Näslund I., Degerman E. & Nordwall F. (1998) Brown trout (*Salmo trutta*) habitat use and life history in Swedish streams: possible effects of biotic interactions. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 1034–1042.

Nilsson C., Lepori F., Malmqvist B., Törnlund E., Hjerdt N., Helfield J.M., Palm D., Östergren J., Jansson R., Brännäs E. & Lundqvist H. (2005) Forecasting environmental responses to restoration of rivers used as log floatways: An interdisciplinary challenge. *Ecosystems* **8,** 779-800.

Olsson T.I. & Persson B.G. (1986) Effects of gravel size and peat material concentrations on embryo survival and alevin emergence of brown trout (*Salmo trutta* L.). *Hyrobiologia* **135,** 9-14.

Olsson T.I. & Persson B.G. (1988) Effects on deposited sand on ova survival and alevin emergence in brown trout (*Salmo trutta* L.). *Archiv fur Hydrobiologie* **113,** 621-627.

Östergren J. (2007) *Migration biology and genetic population structure of anadromous salmonids (*Salmo salar & S. trutta *L.) in northern Swedish rivers.* PhD-thesis, Umeå: Swedish University of Agricultural Science, 31 pp.

Pihlaja O., Julkunen M., Niemelä E. & Erkinaro J. (1998) Changes in density of introduced sculpin, *Cottus gobio* L., and its impact on juvenile Atlantic salmon, *Salmo salar* L. densities in a subarctic salmon river in northern Finland. *Fisheries Management and Ecology* **5,** 189–199.

Savino J.F. & Henry M.G. (1991) Feeding rate of slimy sculpin and burbot on young lake charr (*Salvelinus namaycush*): effect of rock size. *Journal of Freshwater Ecology* **6,** 151-170.

Tabor R.A., Brown G.S. & Luiting V.T. (2004) The effect of light intensity on sockeye salmon fry migratory behavior and predation by cottids in the Cedar River, Washington. *North American Journal of Fisheries Management* **24,** 128-145.

Thorstad E.B., Økland F. & Finstad B. (2000) Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *Journal of Fish Biology* **57,** 531-535.

Utzinger J., Roth C. & Peter A. (1998) Effects of environmental parameters on the distribution of sculpin *Cottus gobio* with particular consideration of the effects of obstructions. *Journal of Applied Ecology* **35,** 882-892.

Webb J.H., Fryer R.J., Taggart J.B., Thompson C.E. & Youngson A.F. (2001) Dispersion of Atlantic salmon (*Salmo salar*) fry from competing families as revealed by DNA profiling. *Canadian Journal of Fisheries and Aquatic Sciences* **58,** 2386-2395.

Witzel L.D. & MacCrimmon H.R. (1983) Embryo survival and alevin emergence of brook charr, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. *Canadian Journal of Zoology* **61,** 1783-1792.

Figure legends

Figure 1. Map of the River Vindelälven, the tagging location and Umeå Marine Research Station (UMF). Shaded area indicates the distribution of European sculpin within the River Vindelälven.

Figure 2. Schematic drawing of the stream aquaria and structure of the artificial spawning redd with the location of the salmon egg pocket.

Figure 3. Proportion of electric fishing sites dominated by (A) water velocity [categories 1-3 represent 0-0.2, 0.2-0.7 and >0.7 $m \cdot s^{-1}$ respectively] and substrate size categories [4-9 represent 2–10, 10–20, 20–30, 30–40, 40–200 cm in diameter and bedrock respectively]. Grey and white bars indicate electric fishing sites located within and outside the European sculpin distribution area.

Figure 4. Predation rate (A) and growth (Daily Growth Coefficient (DGC)) (B) (mean ± standard error) of European sculpin on Atlantic salmon eggs in artificial spawning redds constructed of different substrate sizes. Bars with the same letters are not significantly different.