Small larvae in large rivers: observations on downstream movement of European grayling *Thymallus thymallus* during early life stages

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Behaviour of early life stages of the salmonid European grayling *Thymallus thymallus* was investigated by assessing (i) the timing of larval downstream movement from spawning areas, (ii) the depth at which larvae moved, and (iii) the distribution of juvenile fish during summer in two large connected river systems in Norway. Trapping of larvae moving downstream and electrofishing surveys revealed that *T. thymallus* larvae emerging from the spawning gravel moved downstream predominantly during night, despite light levels sufficient for orientation in the high-latitude study area. Larvae moved in the water mostly at the bottom layer close to the substrate, while drifting debris was caught in all layers of the water column. Few young-of-the-year still resided close to the spawning areas in autumn, suggesting large-scale movement (several kilometres). Together, these observations advocate that there may be a deliberate, active component to downstream movement of *T. thymallus* during early life stages. This research signifies the importance of longitudinal connectivity for *T. thymallus* in Nordic large river systems. Human alterations of flow regimes and the construction of reservoirs for hydropower may not only affect the movement of adult fish, but may already interfere with active movement behaviour of fish during early life stages.

Key-words: behaviour; connectivity; drifting larvae; large river systems; spatial distribution; salmonid fish

INTRODUCTION

Fish in river- and lake systems disperse and migrate over large spatial scales, during various life stages and for a wide variety of reasons (e.g. Linløkken, 1993; Pavlov *et al.*, 2008; Brönmark *et al.*, 2014). Fish movement can positively affect growth rates (Gillanders *et al.*, 2015), and reduce predation risk (e.g. Skov *et al.*, 2011; Skov *et al.*, 2013) and competition (Vøllestad *et al.*, 2002). Movement can also increase predation risk and energy expenditure (e.g. Chapman *et al.*, 2012; Chapman *et al.*, 2013), and is therefore not always an active choice. Animals living in moving habitats like rivers and the sea can also face unintentional movement. For fish species in fast-flowing rivers it can be difficult to regulate their position in the water during early life stages. Embryos, larvae, or juveniles in rivers often drift downstream along with water currents, which can lead to long-distance displacements (Brown & Armstrong, 1985; Pavlov, 1994; Humphries *et al.*, 2002; Pavlov *et al.*, 2008). Downstream movement forms an important phase in the life cycle of many riverine fish throughout the world (Reichard *et al.*, 2001; Reichard *et al.*, 2002; Oesmann, 2003; Lechner *et al.*, 2014).

Two contrasting hypotheses explain downstream movement of fish during early life stages. Movement can be either passive drift because of living in a moving habitat, or an active behaviour (Pavlov, 1994; Humphries *et al.*, 2002; Gilligan & Schiller, 2003; Lechner *et al.*, 2014). Although the assumptions of the two hypotheses are not necessarily mutually exclusive, contrasting their assumptions can improve our mechanistic understanding of fish movements during early life stages. The *passive drift hypothesis* assumes that movement is an involuntary consequence of living in river systems where there is always a downstream movement of water. Passive movement of larvae is also referred to as passive downstream dispersal, passive displacement or obligatory drift (Humphries *et al.*, 2002; Pavlov *et al.*, 2008). Passively drifting larvae, such as Murray cod *Maccullochella peelii* (T. L. Mitchell, 1838), golden perch *Macquaria ambigua* (J. Richardson 1845) and probably common carp *Cyprinus carpio* L. 1758, are unable to control their position in the water column (Humphries *et al.*, 2002; Huey *et al.*, 2014). If larval swimming capacity remains too low to avoid movement downstream, displacement of emerging fish may occur before habitat choice is possible (Wolter & Sukhodolov, 2008).

Alternatively, the *active movement hypothesis* assumes downstream movement is a facultative behaviour (as discussed in Humphries *et al.*, 2002). This is also called active dispersal (although not entirely by locomotion) or controlled downstream migration (assuming larvae return to the spawning areas as adults, Pavlov *et al.*, 2008). According to this hypothesis larvae deliberately migrate downstream towards favourable nursing areas making use of water currents, and movement is actively used for transport between spawning and nursery areas during early life stages. This hypothesis explains the behaviour of for example flathead gudgeon *Philypnodon grandiceps* (Krefft, 1864), common bream *Abramis brama* L. 1758 silver bream *Abramis bjoerka* L. 1758 and roach *Rutilus rutilus* L. 1758 (Humphries *et al.*, 2002; Reichard *et al.*, 2004).

Here these two hypotheses are investigated to enhance our understanding of larval movement in a potamodromous population of European grayling *Thymallus thymallus* L. 1758 in southeastern Norway. *T. thymallus* is a spring-spawning, rheophilic salmonid fish, that predominantly spawns in oxygen-rich gravel of fast-flowing cold rivers and tributaries (Northcote, 1995). Upon hatching, larvae stay in the substrate for multiple days before emerging in response to changes in light and temperature conditions (Scott, 1985; Bardonnet & Gaudin, 1990a). Emerged larvae move downstream (e.g. Bardonnet & Gaudin, 1990b; Bardonnet *et al.*, 1991; Grimardias *et al.*, 2012), however, empirical data on how long, where and why *T. thymallus* moves during early life stages are scarce.

Two underlying assumptions of the hypotheses are investigated, involving the (i) timing of larvae movement and the (ii) position of larvae in the water column. First, larvae of many fish species have the tendency to move predominantly during the night (Jurajda, 1998; Carter & Reader, 2000). *T. thymallus* in southern European regions emerge on a diel pattern from the gravel in response to light and water temperature fluctuations, resulting in movement during the night (Bardonnet & Gaudin, 1990b; Bardonnet & Gaudin, 1991; Bardonnet *et al.*, 1991). This could be caused by (i) loss of visual orientation in the dark, because visual acuity in fish improves during ontogeny and is still relatively low in early life stages (Hubbs & Blaxter, 1986; Nunn *et al.*, 2012), or (ii) active behaviour of larvae preferring movement under safer, lower light conditions (Bardonnet, 1993; Pavlov, 1994). While at more southern latitudes disorientation during complete darkness is a likely cause, during the Nordic summers pertinent to our study area sufficient light for orientation is available during both night and day. If under these conditions movement still occurs predominantly during the night, this would add support to the hypothesis that downstream movement involves an active behaviour. The second assumption focuses on where in the water column larvae mostly move. Following the passive drift hypothesis, larvae are expected at the same depth as floating debris with similar buoyancy, because they are unable to concentrate their movement at any specific depth. If downstream displacement is active behaviour, movement could be confined to a depth in the water column with energetic or survival benefits.

The aim of this study was to better understand the role of movement of *T. thymallus* during early life stages. Assumptions underlying passive and active movement patterns are contrasted, and possible habitat selection by larvae was assessed three-months post-hatching. Lack of knowledge about movements and distributions of larvae and juveniles in large river systems hampers our possibilities for targeted management to assess the impact of e.g. altered water discharge, establishment of reservoirs and dams in river systems due to new hydropower development. Specific objectives were therefore to (i) document the magnitude of larval movement at northern latitudes with continuous light conditions, (ii) assess the timing and duration of larval movement in large river systems, and (iii) present information on juvenile distributions in the study system.

MATERIAL AND METHODS

STUDY AREA

The study area is an unfragmented 20 km section of the Gudbrandsdalslågen River (hereafter Lågen) and a 15 km stretch of the Otta River in southeastern Norway, which creates a Y-shaped system with two barriers for upstream migration (Fig. 1). Lågen River is one of Norway´s largest rivers, with a catchment area of 11 567 km^2 and a mean annual discharge at Rosten waterfalls of 32.7 $m^3 s^{-1}$ (monitored by Oppland Energi AS, 2009). The river is fed by snowmelt in high-altitude mountain areas and the mean annual spring flood is 311 $m^3 s^{-1}$. At Otta City, Lågen River is joined by the Otta River, which has a catchment area of 4 150 km^2, a mean annual discharge of 111 $m^3 s^{-1}$ and mean annual spring flood of 650 $m^3 s^{-1}$ at the Eidefoss power plant (Museth *et al.*, 2011). Detailed river discharge data for 2013 and 2014 were obtained from Oppland Energi AS (Fig. 2).

Several *T. thymallus* spawning sites have been identified in both rivers and described previously (Museth *et al.*, 2011; Junge *et al.*, 2014). The two largest spawning areas in Lågen River are immediately downstream of the Rosten Waterfalls and immediately downstream of the confluence of the two rivers. In Otta River, the largest spawning area for *T. thymallus* is directly downstream of the Eidefoss Dam (Fig. 1).

Light availability for orientation by larvae was lower during the night than during daytime in the studied area, but at the latitude of the study site it never becomes completely dark. Hourly illumination data were obtained using a pyranometer (W m^{-2}) from Otta Meteorological Station (61.7782N, 9.5413E, Meteorological Institute, Station no. 16040) for June and July 2015. Average illumination in June and July was 47.8 W m^{-2} during the night (2200 to 1000 h), which was 45% of the average of 105.4 W m^{-2} during daytime (1000 to 2200 h).

STUDY SPECIES

T. thymallus is a salmonid that prefers fast-flowing rivers, but is also found in lakes. In early spring, adults typically migrate toward fast-flowing river sections or from lakes into tributaries for spawning in oxygen rich microhabitats (Northcote, 1995; Sempeski & Gaudin, 1995). Eggs are deposited in the substrate and hatch after 264-320 degree days (duration varies by population, Bardonnet & Gaudin, 1991; Haugen, 2000). *T. thymallus* is highly fecund and produces relatively small eggs for salmonids (2-4 mm), that stay close to the surface of the substrate until hatching (Northcote, 1995). After hatching, larvae move into the substrate where they spend four to eight days (Scott, 1985; Bardonnet & Gaudin, 1990a). Larvae emerge from the gravel in response to light and temperature (Bardonnet & Gaudin, 1990a). In the study area, *T. thymallus* spawn during a relatively short period around late May and early June (Museth *et al.*, 2009). The main predators of larvae in the study system are brown trout *Salmo trutta* L. 1758 and adult *T. thymallus*. Except for the European minnow *Phoxinus phoxinus* L. 1758, *S. trutta* and *T. thymallus* are the only species in the river system, and both can occur at high densities. Both species are visual predators, implying that larvae are safest close to the gravel bed of the river where their silhouette is least visible.

MONITORING DOWNSTREAM DRIFT OF LARVAE

Downstream movement of *T. thymallus* larvae was monitored throughout the study area during the summer seasons of 2013 (June 13 – July 13) and 2014 (June 17 – July 7, Fig. 1).

During both years, larvae were caught by filtering water in traps constructed of a 0.10 m section of a polyvinyl chloride (PVC) pipe with a diameter of 0.16 m. The circular PVC formed an open surface of 0.020 m^2 to which a 1.0 m long × 0.34 m wide section of coiled nylon net (mesh = 0.9 mm) was glued. The coiled net was connected to the circular ring of PVC to form a 1.0 m long conically shaped tube: water entered the PVC ring that faced the upstream direction of the river, and exited through the net that was closed at the downstream end by gluing the nylon net together. Two holes were drilled in the PVC of each net so they could slide over 2.0 m long steel bars that were vertically placed into the gravel bed. Cable ties ensured the correct height of each trap on its steel bar. At a water velocity of 0.5 m s^{-1} (it ranged from 0.2 to 0.8 m s^{-1} during the study period) the volumetric flow rate (Q) filtered by each trap would be 0.010 m^3 s^{-1} (or 10 litres per second). For security and practical reasons all traps were placed between three and 10 m from one side of the riverbank (maximum river width = 120 m).

Traps were attached to steel bars placed at seven possible locations in the river system, where access was feasible (locations 1 to 7 indicated in Fig. 1). Each bar could hold three traps of which the depth could be regulated. In the pilot year 2013, the main aim was to document downstream movement and the duration of this movement. For this, only two traps were used per sampling location: larval movement was monitored at location 2 in Otta River, location 4 at the confluence and location 7 in Lågen River (Fig. 1). At each location, one of the traps rested on the substrate of the river and one trap was mounted just below the water surface. In 2014, a more extensive sampling plan was carried out by sampling all seven locations (Fig. 1), and an additional trap was fitted at a mid-position relative to the water depth (ranging from 0.25-0.50 m deep) on the steel bars to monitor the depth of moving larvae in more detail. In both years, all traps were checked and emptied every 24 h between 1200 and 1500 h by immediately sorting their contents in white plastic buckets. During a period of substantial larval movement in 2014 (between the 3rd and 5th of July) the sampling intervals were shortened to 12 h (at 1000 and 2200 h) to examine possible diel patterns.

More aspects of larval movement were monitored in 2014 than in the pilot year of 2013. In 2014, additionally the total length of all sampled larvae (dead and alive) was measured (in mm). Water velocity was measured directly in front of each trap throughout the 2014 season with a pygmy water speed meter (AquaCount, JBS Instruments). On the 3rd and 4rd of July in 2014, all invertebrate larvae, leaves and other organic material (further referred to as "debris") that was collected in the traps was stored at -20° C. Afterwards it was dried for 48 h at 60° C and its dry mass was determined to the nearest gram on a Mettler AE160 (d = 0.1 mg). Larval fish sampling ceased by loss of our sampling equipment in both years, but at these times the catches had already severely declined.

DETERMINING THE DISTRIBUTION OF JUVENILE FISH

To gain insight in the spatial distribution of juvenile fish (fork length between 5 and 25 cm) in the river system, two sections in the upstream part of the study area (see Fig. 1) were surveyed between the 11th and 23rd of September 2013 by boat electrofishing. A Smith Root rafting boat (model Cataraft) was used, equipped with a Smith Root 7.5 kW pulsator. In two sections (I and II, see Fig. 1), respectively 12 and 9 transects with a length of 500 m were surveyed in detail. This produced data on juvenile densities with varying distances to the dominant upstream spawning areas. The electrofishing surveys were conducted by supplying an electrical current to anodes positioned in the water in front of the boat, which created an electrical field with the cathode positioned at the front of the boat´s hull. Stunned fish were captured by one of two dip net-handlers in the front of the boat. Conductivity of the water was 0.53 - 1.01 µS m^{-1}; the output current was 1.1 – 1.9 amps with 1000 V and 60/120 DC.

Catch effort was normalized by calculating the Catch-Per-Unit-Effort (CPUE) as number of fish caught per minute of fishing (minutes with electric voltage in the water registered by the pulsator). Total effort was 6 h and 2 minutes. Captured fish were measured for total length (in mm) before release back into the river, which was used as our best possibility to distinguish age classes 0+, 1+ and >1+ (no other age data was available). All necessary fishing permissions were obtained and the same electrofishing equipment, technique and specially trained personnel performed the surveys.

STATISTICAL ANALYSES

The number of larvae per m^3 of filtered river water was compared to the number expected based on a uniform distribution with equal numbers of larvae per water volume within each river. Fisher´s exact tests for count data were used to test for statistical differences between all possible combinations of water depths per river. Possible effects of river, depth in the water column and water velocities on drift of debris were assessed by linear mixed-effects modelling using package nlme (Pinheiro *et al.*, 2015). Each sampling event (unique combination of location and moment) was included as random factor so that comparisons were only made between depths in the water column within otherwise identical circumstances. All possible interactions among fixed factor river, fixed factor depth in the water column and continuous variable water velocity were initially included in the models, and removed if statistically insignificant based on Likelihood Ratio Tests between models with and without the interaction (i.e., backwards selection). Differences between levels of factors were assessed by Tukey-posthoc tests using package multcomp (Hothorn *et al.*, 2008). Debris dry mass was ln-transformed to ensure homogeneity of residual variances. All statistics were performed in R version 3.2.3 for statistics (R-Development-Core-Team, 2016).

RESULTS

STUDY OF DOWNSTREAM MOVEMENTS

T. thymallus larvae were caught moving downstream in two large rivers and at their confluence in both 2013 and 2014 (Fig. 2, Fig. 3). Catch occurred over 10 days in 2013 (June 26 – July 6, total number of larvae caught: n = 41) and 13 days in 2014 (June 25 – July 7, total caught: n = 107). Larval length was 15.9 ± 1.0 mm (mean ± S.D., n = 67 measured in 2014, Fig. 3). Twenty-three larvae were caught during the intensified 12 h-sampling intervals in 2014. Of those, 20 larvae (87%) moved during the night or early morning (between 2200 and 1000 h) and three larvae (13%) during daytime (between 1000 and 2200 h). Movement was significantly more frequent during the night compared to an expectation of equally proportioned movement during daytime and night (Chi-squared test, $\chi^2 = 12.56$, *d.f.* = 1, $P < 0.001$).

In 2014, the number of larvae per cubic meter water statistically differed among depths in both rivers, with 54% of all caught larvae moving directly over the river bottom (statistical results indicated in Fig. 4a). Debris dry mass (g) was significantly higher in Lågen River than Otta River (linear mixed-effects model, $F_{1,6} = 44.4$, $P < 0.001$, Fig. 4b). In Otta River, the amount of drifting debris did not vary with water depth (all three Tukey posthoc comparisons on linear mixed-effects model, $|Z| < 1.85$, $P > 0.42$). In Lågen River, more debris was caught in traps resting on the bottom than traps at the water surface (Tukey posthoc comparison, $Z = -2.96$, $P = 0.03$). However, debris dry mass did not differ between the middle and the bottom traps (Tukey posthoc comparison, $Z = -2.26$, $P = 0.20$) nor between the middle and the surface (Tukey posthoc comparison, $Z = -0.70$, p = 0.98). Water velocity did not differ between the sampling locations in the rivers (linear mixed-effects model, $F_{1,72} = 0.83$, $P = 0.37$, Fig. 4c), but was lowest at the bottom in both rivers (linear mixed-effects model, $F_{2,73} = 14.84$, p <0.0001, Tukey-posthoc comparisons middle-bottom: $Z = 4.04$, p < 0.001, middle-surface: $Z = 1.27$, p = 0.41, surface-bottom: $Z = 5.3$ p < 0.001).

SPATIAL DISTRIBUTION OF JUVENILE *T. THYMALLUS*

Juvenile *T. thymallus* caught by boat electrofishing in autumn varied between 5 and 25 cm in length (n = 62). The frequency distribution of the juveniles suggested that this involved thirty-six young-of-the-year (0+, <10 cm), eighteen 1+ (10 – 18 cm) and eight >1+ (18 – 25 cm) individuals. In total, 35 *T. thymallus* were caught in Lågen and 27 in Otta River, with respectively 28 and 8 young-of-the year in Lågen and Otta River (for CPUE details, see Fig. 5a). During the same surveys, 418 juvenile *S. trutta* were caught, including 308 young-of-the-year (Fig. 5b). Average CPUE for young-of the year was lower for *T. thymallus* (mean ± S.D. 0.10 ± 0.18) than for *S. trutta* (mean ± S.D. 0.78 ± 0.50) during the same surveys. CPUE did not correlate to the proximity of identified upstream spawning areas (Pearson's product-moment correlations, Otta River: r = 0.10, *d.f.* = 10, P = 0.75, Lågen River: r = -0.07, *d.f.* = 15, P = 0.78).

DISCUSSION

In two large Nordic rivers *T. thymallus* larvae moved downstream mainly during night and close to the bottom layer of the river substrate. Despite the presence of large spawning areas upstream, only few young-of-the-year were caught by electrofishing surveys within the study area in autumn. This data is mostly in accordance with the active movement hypothesis for larvae movement: larvae may benefit from actively moving downstream to suitable nursery areas. Active movement is in accordance with previous observations in other fish species such as flathead gudgeon, common and silver bream, and roach (Pavlov, 1994; Humphries *et al.*, 2002; Reichard *et al.*, 2004). Previous work has mainly focused on movement of fish larvae in slower-flowing river systems or smaller streams and tributaries (e.g. Bardonnet *et* *al.*, 1991; Pavlov, 1994; Reichard *et al.*, 2004; Zitek *et al.*, 2004), likely because of the practical difficulties when working in large river systems. This study suggests that larval movement in *T. thymallus* is an important means for transportation of early life stages towards suitable nursery areas in both large and small river systems (Brown & Armstrong, 1985; Pavlov *et al.*, 2008), and that it involves a behavioural, deliberate component. This sheds light on movement of a lesser-studied species in a type of study system for which few studies exist.

ACTIVE VERSUS PASSIVE DOWNSTREAM MOVEMENT

This study contrasted active and passive larval movement based on the timing and depth of captured larvae. Firstly, *T. thymallus* larvae moved predominantly during night, even though sufficient light was likely available at night in our Nordic summers. Larvae moved at a size where they likely already have substantial visual acuity (Miller *et al.*, 1993). This makes reduced visibility a less likely cause of nocturnal larval drift. However, this pattern of nocturnal drift was documented during just three days of sampling, and more sampling is necessary to determine the generality of this pattern. Larvae most likely started drifting in response to water temperatures (Bardonnet & Gaudin, 1991), or chose to drift during low light conditions to minimize encounters with visual feeding predators. Based on these observations in our Nordic study area, disorientation seems not a major cause of *T. thymallus* larval movement in the study system. The observations on the timing of movement mostly supported the active movement hypothesis.

Secondly, larvae were not randomly present in the water column. In both rivers, the surface and middle traps filtered a larger water volume per minute than the deepest trap, but most larvae were caught in the traps deepest in the water column. In contrast, traps of varying depths caught similar sizes, types and amounts of debris. Although potential differences in buoyancy between debris and larvae prohibits a direct comparison, the observation that not all debris was caught in the deepest traps strengthens the view that larvae had some control over their position in the water column. This ability is known for many aquatic animals, including many fish larvae as shown by both modelling (Schludermann *et al.*, 2012) and empirical studies (Grimardias *et al.*, 2012). Having some capacity to swim can help avoid predation, enhance foraging, and influence interactions with conspecifics (Wolter & Arlinghaus, 2003). These results are in line with the estimated burst swimming capacity (i.e. of very short duration) of almost 0.20 m s^{-1} (see Wolter & Arlinghaus, 2003 for an extensive review) of larvae of up to 19 mm in this study. Compared to the water velocities in the study system, burst swimming could enable them to enter or exit faster-flowing currents in the studied river system and thus regulate their depth. The position of moving larvae in the studied rivers mainly supported the active movement hypothesis, and suggested larvae were capable of entering and exiting faster flowing currents in the river.

SPATIAL DISTRIBUTION OF JUVENILE *T. THYMALLUS*

Juvenile *T. thymallus* were only encountered in low numbers in the study area, despite heterogeneity in river gradients, associated flows and large dominant spawning areas upstream in both studied river systems. This was in strong contrast with encountering many *S. trutta* young-of-the-year during the same surveys, with a similar catchability (Bohlin *et al.*, 1989) and similar spawning areas in the studied system (Museth *et al.*, 2011). The spatial distribution of the few *T. thymallus* juveniles that were present did not reflect the presence of the large spawning areas in the most upstream parts of the studied rivers. Proximity to spawning sites did not increase juvenile densities, such as for example in Atlantic salmon *Salmo salar* L. 1758 (Beall *et al.*, 1994). Desertion of spawning tributaries by all young-of-the-year has previously been documented for *T. thymallus* in France (Bardonnet *et al.*, 1991), and a similar pattern seems to occur in the large rivers of our study area. Nursery areas for young fish should at the minimum provide suitable hydraulic and trophic conditions that are relatively free of predators (Cattanéo *et al.*, 2014). Young *T. thymallus* in the study system were therefore expected to prefer shallow (10–30 cm) water with low current velocities (<0.15 m s^{-1}), with substrates smaller than 2 mm and variable vegetation cover (10–70%), and will mostly reside between 0.2 and 1 m from the river bank (Nykänen & Huusko, 2003). According to these characteristics, suitable nursery areas were present in the study system. However, few juveniles were present. Whether these moved downstream actively or passively remains a question for future studies.

TIMING OF MOVEMENT

Larval movement occurred only during relatively short periods in the Nordic study area, which contrasts to longer periods in *T. thymallus* at more southern latitudes (e.g. Grimardias *et al.*, 2012). However, a relatively short movement season corresponds very well to the known short spawning periods in Nordic regions (Museth *et al.*, 2011; Junge *et al.*, 2014). Although both studied river systems have two major annual flooding periods, which could be an alternative cause of movement if larvae were washed away during floods (Lechner *et al.*, 2014), no causal relationship between elevated discharge of the rivers and the timing of larval movement was detectable in the discharge data. Larvae moved mainly outside the major flooding periods in both rivers, and their timing was largely similar between the years despite clear differences in the timing of flooding. The most likely cause of the short movement period is therefore the short spawning period in the studied area, which is in line with the similar developmental stage of all captured larvae. A stronger relation between the timing of movement and the timing of spawning than between movement and flooding, further supports an active behavioural component to larval movement (Pavlov, 1994; Reichard *et al.*, 2004; Zitek *et al.*, 2004; Reichard & Jurajda, 2007).

CONCLUSION

In conclusion, this study suggests that *T. thymallus* in a large river systems are at least partly able to control their downstream movement at very young ages. Observing large-scale downstream movement suggests that this process is essential in the life cycle of fish in large river systems. Furthermore, it emphasises how man-made reservoirs and flow regulation in rivers may disrupt salmonid life cycles by altering hydrology and creating barriers to movement. Understanding the ecology of movement is essential for effective management of mobile fish species, such as *T. thymallus*.

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Figure captions

Figure 1: The study area around the confluence of the Gudbrandsdalslågen River and Otta River at Otta City, including two barriers to upstream migration (red triangles). Drift sampling locations (blue stars), main spawning areas (orange squares, accounting for at least 80% of all spawning areas) and electrofishing transects (green dashes) are indicated.

Figure 2: The timing of larval drift in relation to river discharges in 2013 and 2014, for Lågen River (2013: solid black line, 2014: dark grey line), and Otta River (2013: light grey dashed line, 2014: black dashed line).

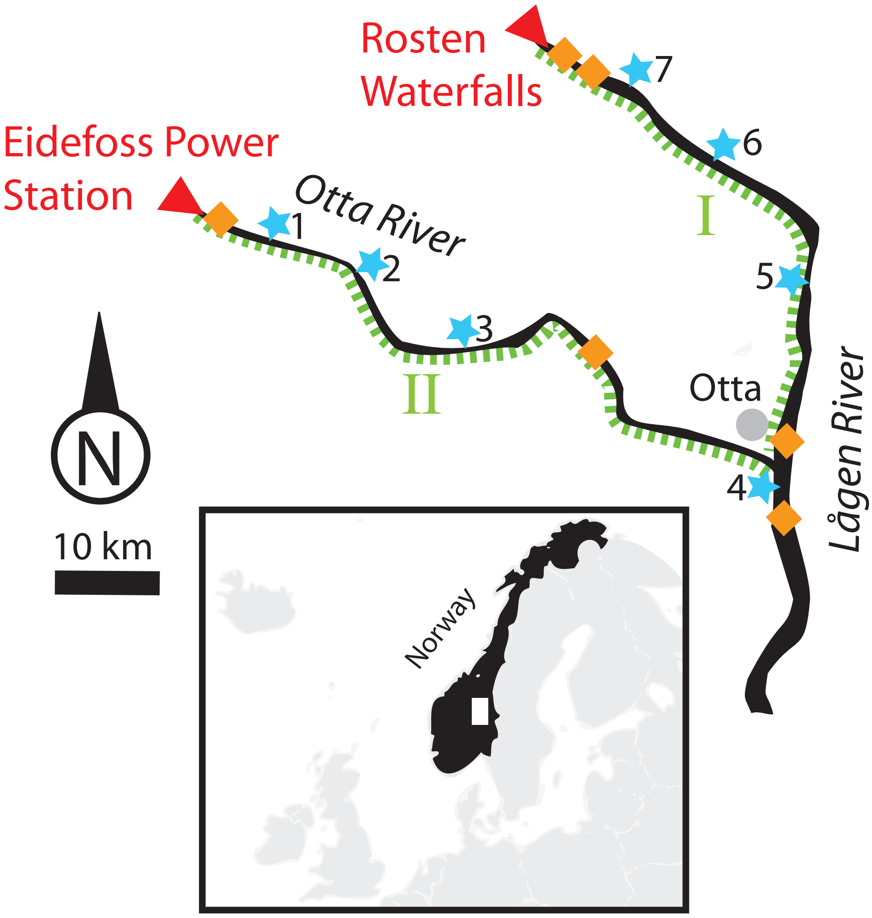
Figure 3: The number of *T. thymallus* larvae caught over time in Lågen River (2013: white, 2014: dark grey) and Otta River (2013: light grey, 2014: black). Note that sampling effort differed between years, resulting in variation in number of larvae caught but not in the timing of drift. Inset shows the total length distribution of all larvae caught in 2014.

Figure 4: Effects of depth in the water column in the two river systems on (a) number of larvae caught per m^3 of water filtered in 2014 depicted by the horizontal bars, with the actual counts indicated at the end of each bar, (b) debris dry mass collected during two sampling occasions ($n = 48$ samples, depicted with a log-scale horizontal axis to visualize variances), (c) water velocities ($n = 111$ measurements). Bars in the panels that do not share a common letter differ significantly at the $\alpha = 0.05$ level (see Results for details).

Figure 5: Catch-Per-Unit-Effort for juvenile (**a**) *T. thymallus* and (**b**) *S. trutta* of three age classes (0+ as light grey, 1+ as dark grey, 2+ as black) in relation to distance from the most

upstream migration barrier in Otta River and Lågen River. In both rivers more *S. trutta* were caught than *T. thymallus*.

635 **Figures**



636

637 Figure 1

638

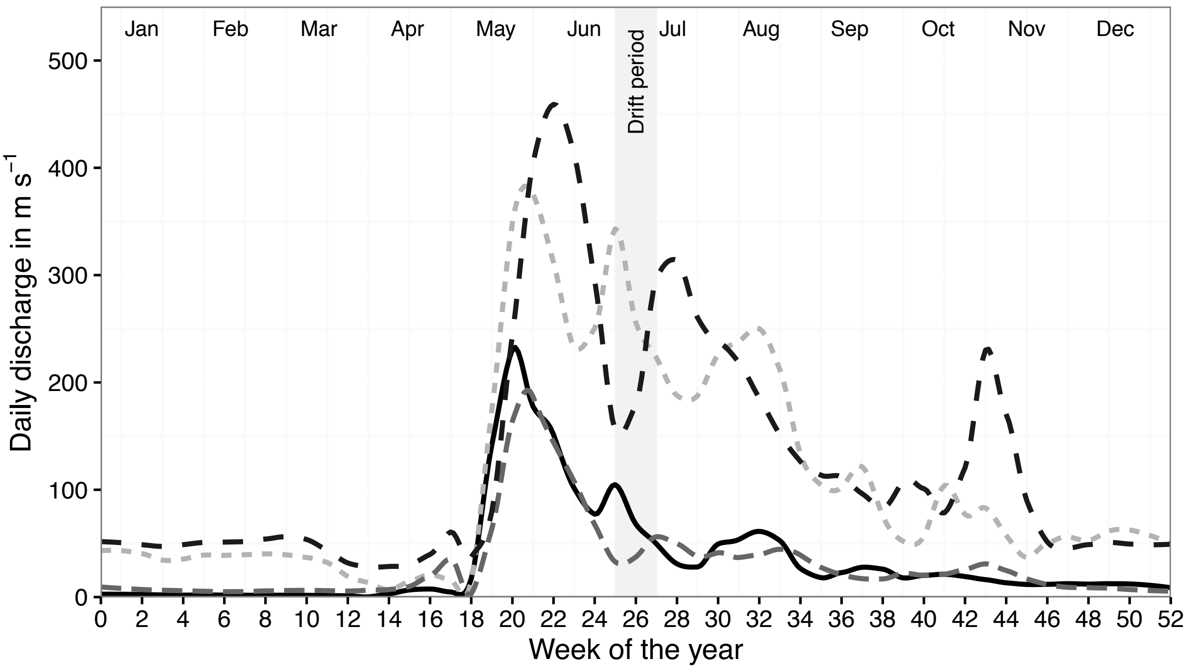
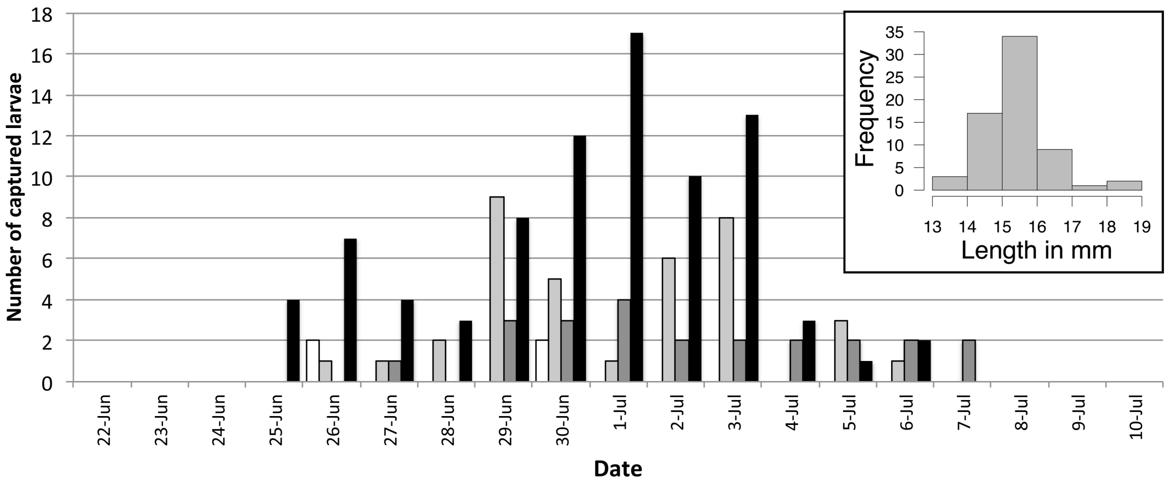

Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Drift period
Daily discharge in m s⁻¹
0
100
200
300
400
500
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 50 52
Week of the year

Figure 2



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643 Figure 3

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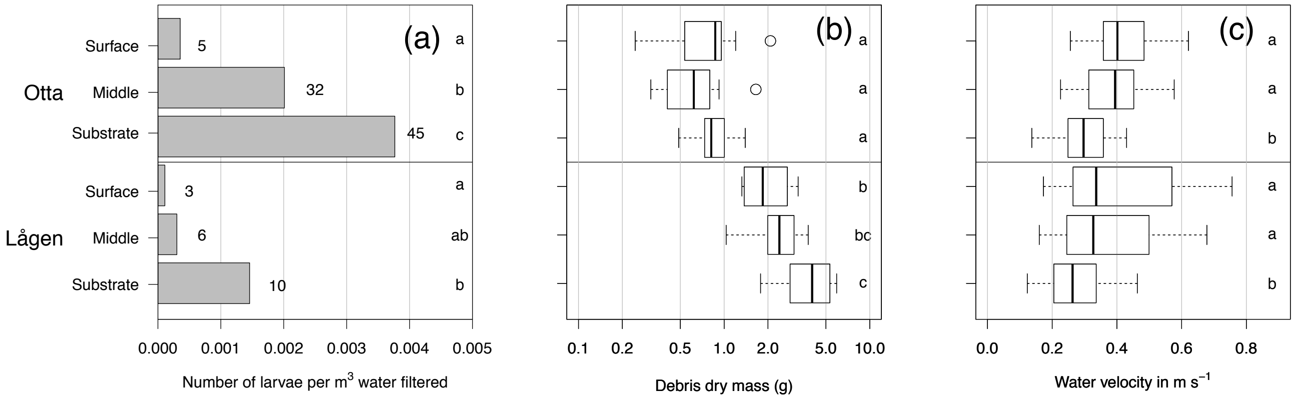

(a)
(b)
(c)
Otta
Lågen
Surface
Middle
Substrate
Surface
Middle
Substrate
5
32
45
3
6
10
a
b
c
a
ab
b
a
a
a
b
bc
c
a
a
b
a
a
b
0.000 0.001 0.002 0.003 0.004 0.005
Number of larvae per m3 water filtered
0.1 0.2 0.5 1.0 2.0 5.0 10.0
Debris dry mass (g)
0.0 0.2 0.4 0.6 0.8
Water velocity in m s−1

Figure 4

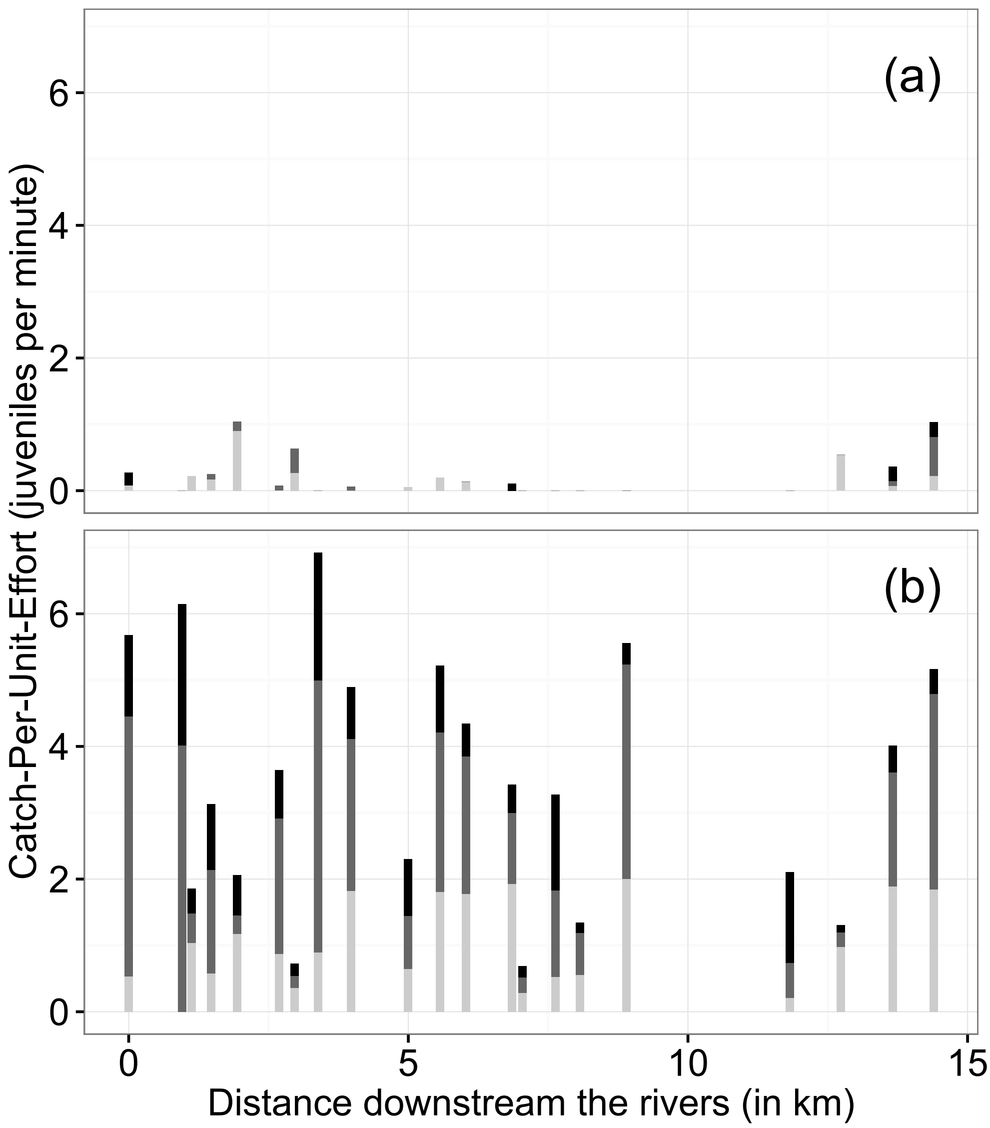
(a)
(b)
6
4
2
0
Catch-Per-Unit-Effort (juveniles per minute)
0
5
10
15
Distance downstream the rivers (in km)

Figure 5