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Downstream Drift of Grayling (*Thymallus thymallus*) Fry in the Rivers Otta and Gudbrandsdalslågen: Temporal and Spatial Patterns

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– Temporal and spatial patterns

Preface

This thesis marks the end of my master degree in Natural Resource Management at the Department of Ecology and Natural Resource Management (INA), Norwegian University of Life Sciences (NMBU).

This thesis was proposed by Jon Museth at NINA Lillehammer who through environmental impact assessments in the Otta/Gudbrandsdalslågen river system observed a large migration system of grayling, with high abundances of young fish in downstream sections and a desertion of upstream spawning sites. After 4 years of hearing about this hypothesis, I was convinced and wanted to investigate the phenomenon I had heard so much about.

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Abstract

The object of this study was to investigate drift of grayling fry in two large Norwegian inland rivers. Previous studies of migrations and area use of grayling in the Otta-Gudbrandsdalslågen river system made the area well suited for further studies. There is little knowledge about the migrations of year-of-young grayling in such systems, and how these migrations influence the distribution of adult fish.

To investigate and compare the drift between Otta and Gudbrandsdalslågen rivers, drift traps were made, and distributed over four stations at different depths in both rivers in 2014. The traps was checked and the contents sorted every 24 hour period, with 12 hour sampling periods at selected stations to explore potential diel patterns in the drift. The captures of drifting larvae were modelled to investigate the influence of different environmental factors and the results were compared between rivers.

Drift of grayling larvae was observed over a short time period of 12-13 days. The larvae mainly drifted at night, deep in the water column. The sum of degree days ($°D > 5° C$) was the environmental factor best explaining the drift of grayling larvae. There were between-river differences in both the spatial distribution of the drift and observed growth in larvae during the study period. Grayling larvae drifted through the whole study area in Otta, while drift only was observed at the uppermost and lowest station in Lågen. The length of trapped grayling larvae in Otta stayed the same during the study period, while growth was recorded in Lågen, possibly due to the differences in distribution of nursery areas between the rivers.

The observations of drift made in this study are related to the early life history strategies of the grayling in the river system. The grayling is adapted to ensure drift dispersal of larvae from high velocity spawning sites to slow flowing nursery habitat. This can be hypothesized to be an underlying factor in the motivation behind the potamodromous migration cycle of the grayling in the river system. Hydropower development and loss of connectivity will arguably influence the drift of larvae and the motivation behind migration of grayling, possibly changing the selection from favoring migration towards stationary behavior.

1 Introduction

Migrations are "adaptive, long-distance movements that occur predictably in the life cycle of a species" (Smith 1985). They are considered as an adaptation to increase growth, survival and abundance of freshwater fishes (Northcote 1984). Migrations has been formed as a result of separation between different seasonal habitats (i.e. spawning, feeding, nursery and /or overwintering areas) (Northcote 1984), and is the main factor influencing the spatial distribution of populations (Zitek et al. 2004). For migrations as an adaptation to evolve, the cost of migration must be less than the benefit from using the separated habitats (Smith 1985). Migrations are common among freshwater fish species, but varies greatly in distance, timing and the proportion of the populations migrating (Pavlov et al. 2008). Rivers are characterized by their major driving force, the downstream flow of water. It defines, manipulates and forms the dynamics within the lotic ecosystems (Allan & Castillo 2007) and influences the evolution of life history strategies for riverine fish species (Winemiller 1989). Hence, fish migration behavior is commonly influenced by "its relation to the system of water currents in the area occupied by that population" (Pavlov 1994). The variation in flow is hypothesized to be the driving force behind reproductive strategies for fish in lotic communities (Humphries et al. 2002). Migrations in general, and especially drift of fry, can potentially reduce the effect of environmental variance on the reproductive success (Leggett 1985). The active use of water currents to assist drift of fish fry might be adaptive for many species of fish (Smith 1985). The downstream transport of larvae from spawning areas to nursery areas can hypothetically be described as an adaptation to the lotic environment, a mechanism that enables the fish fry to exploit the most favorable habitat (Pavlov 1994). It is now understood that larval behavior has a significant impact on the dispersal for many riverine fish species (Brown & Armstrong 1985; Pavlov 1994), and drift of young fish is assumed to be important to transport young fish from spawning sites to nursery areas (Bunn & Arthington 2002; Sonny et al. 2006). There is little knowledge about the life-history dynamics of freshwater migrating (potamodromy) fish species, especially when it comes to migrations and what these migrations mean both on an individual and a population level (Mallen-Cooper 2000). Little is known about the factors, both abiotic and biotic, influencing the displacement of fish larvae (Pavlov et al. 2008) and the motivation behind this downstream transport of larval fish is largely unknown (Pavlov 1994; Humphries et al. 2002).

Several terms have been used to describe early downstream migration of fish. Some authors use the term downstream migration, while others use drift or downstream displacement. Pavlov et al. (2008) defines downstream movements of young fish as migration when the fry actively enters the stream flow as means of downstream transport. When there is no evidence for active behavior, Pavlov et al. (2008) uses the term passive migration, or just drift. Whereas it earlier was assumed that the drift of riverine fish fry was a passive displacement and a direct consequence of rapid or turbulent water flows, the acknowledgement that fry can actively regulate their position is growing (Reichard et al. 2004; Pavlov et al. 2008). Fish fry does not only regulate their positions while drifting. An increasing amount of literature suggests fish fry of many species to actively enter flow zones as a mean of dispersal (Pavlov 1994), supporting the hypothesis that drift is an distributional mechanism for fish. One can argue that the separation between downstream migration and drift seems unnecessary since the fry is transported downstream to new habitat regardless of whether they are forced by currents or actively choose to enter the flow as means of dispersal. To describe drift in general terms, the definition; "downstream transport of aquatic organisms in the current" (Brittain & Eikeland 1988) seems sensible, no matter if there is an active component or the organisms simply drift passive.

We have a better understanding of the motivation behind drift for invertebrates than fish fry. Müller (1954) documented the importance of drift on benthic invertebrate densities. There are support for drift of invertebrates being a behavioral mechanism rather than accidental events (Müller 1974). As for fish, young invertebrates have a larger propensity to drift than adults. This is explained as a dispersal mechanism, and is a part of a "colonization cycle" (Müller 1954; Brittain & Eikeland 1988), similar to the "migration cycle" known for several fish species (Pavlov 1994). In the "colonization cycle" the downstream drift of young individuals is followed by a compensatory upstream migration by adults, termed positive rheotaxis, and it is interpreted as an adaptation to the lotic environment (Brittain & Eikeland 1988). The drift is considered as a regulation mechanism influencing the abundance of young invertebrates in both upstream and downstream sections of rivers (Müller 1954). In sub-optimal habitats invertebrates can drift from less suited habitat conditions and colonize new, more favorable areas downstream (Brittain & Eikeland 1988).

The duration of the drift of fish larvae can vary greatly with hydrological and geological conditions, even between rivers close to each other. Longer drift periods are observed in rivers with slow flowing, shallow zones compared with rivers dominated by high current velocities and with less refuges (Pavlov 1994). The duration of the first drift period for the riverine salmonid European grayling (*Thymallus thymallus*, hereafter just "grayling") is limited to a few days, when the fry leave the spawning grounds and settle in a first-feeding habitat, though there are between-river variations depending on the amount and location of suitable first-feeding habitats (Scott 1985; Bardonnet & Gaudin 1990b; Bardonnet et al. 1991; Grimardias et al. 2012).

Though drift dynamics differ between species (Sonny et al. 2006), a general pattern observed in drifting fish is that larvae of most species drift during dusk or dawn (Gale & Mohr 1978; Brown & Armstrong 1985; Reichard et al. 2001; Reichard et al. 2002b; Sonny et al. 2006) or more general during nighttime (Gustafson-Marjanen & Dowse 1983; Jurajda 1998; Reichard et al. 2001). What we know from earlier studies in southern Europe is that grayling has a diurnal emergence pattern, and they mostly drift during night (Bardonnet & Gaudin 1990b; Bardonnet et al. 1993). The longer days and lighter nights in Norway compared with the earlier studied rivers in southern Europe could influence the diel pattern of the grayling drift.

The longitudinal distribution patterns of fish fry depend both on the spatial distribution of spawning grounds in the river and dispersal of the fry (Robinson et al. 1998). Distribution of drifting larvae is hypothesized to be mainly governed by hydraulics and current velocities (Harvey 1987; Harvey 1991; Pavlov et al. 2008). For grayling fry, who emerges in a habitat with high water velocities not suited as first feeding habitat (Bardonnet et al. 1991; Sagnes et al. 1997; Nykänen & Huusko 2003; Nykänen 2004), the drift carries the fry downstream to more suited river sections. The preferred habitat is shallow, slow flowing zones close to the river bank (Scott 1985; Bardonnet et al. 1991; Nykänen 2004; Grimardias et al. 2012). The drift distances can be both long and short, depending on the distribution of pools and slow flowing sections in the river.

Different fish species show different vertical and horizontal distributions in the water column during drift, implying hydraulics is not the only factor affecting distribution of drifting larvae (Pavlov 1994). It seems that the spatial patterns observed in drifting fish fry depends on both hydraulics and biological factors (Pavlov 1994). Grayling fry have been observed in the upper part of the water column (Scott 1985; Bardonnet et al. 1991), which is similar to observations of cyprinid fry (Brown & Armstrong 1985; Pavlov 1994; Jurajda 1998; Reichard et al. 2004), but uncommon in other salmonids (Bardonnet et al. 1991).

The effect off different factors on drift, both abiotic and biotic are still poorly understood (Pavlov et al. 2008). An increase in discharge usually promotes the drift of fish fry (Harvey 1987; Pavlov 1994; Reichard et al. 2001). Pavlov et al. (2008) argues that the main factors influencing the distribution of drifting fry is hydro-physical and that the most important factor is current velocity, but the effect of discharge and water velocity seems to be dependent on the timing in relation to spawning and emergence (Harvey 1987). The effect of discharge varies between studies, where some studies show a positive effect (Reichard et al. 2001), other studies find no correlation (Robinson et al. 1998; Reichard et al. 2002b; Reichard & Jurajda 2004; Sonny et al. 2006). The role of water transparency on the diel drift pattern varies among studies (Pavlov 1994; Jurajda 1998; Reichard et al. 2001; Sonny et al. 2006). Drift of especially cyprinid fishes is found to peak under increasing temperatures (Sonny et al. 2006). Which factors that affect the temporal and spatial distribution of drifting grayling fry is still unknown. There are indications that light and discharge have an effect, but this varies between studies (Grimardias et al. 2012).

River regulation and the construction of hydropower dams has a negative impact on larval fish distribution (Scheidegger & Bain 1995). Regulation alters the flow regime and impacts the shallow habitats used as nursing habitat for many fish species. For migrating fish species connectivity between habitats is lost and migrations obstructed. The change from fluvial river habitat to a laminate reservoir flow will likely affect drifting fish fry, impairing the dispersal of fish larvae to nursery habitats. The reduced water flow can change the selection towards less migratory genotypes by reducing the benefits of migration (Junge et al. 2014).

The knowledge we have on drift of fish fry is mainly based on observations from slow-flowing river systems dominated by cyprinids and percids (Gale & Mohr 1978; Pavlov 1994; Reichard et al. 2001; Oesmann 2003; Reichard et al. 2004; Zitek et al. 2004; Pavlov et al. 2008) and in faster flowing rivers mostly salmonids, especially brown trout (*Salmo trutta*) (Elliott 1976; Elliott 1987; Bardonnet 1993; Bardonnet et al. 1993; Daufresne et al. 2005) and some studies on grayling (Bardonnet & Gaudin 1990b; Bardonnet & Gaudin 1990a; Bardonnet & Gaudin 1991; Bardonnet et al. 1991; Grimardias et al. 2012). The few larger rivers studied are mostly slow-flowing, species-rich rivers in Middle and Eastern Europe (Pavlov 1994; Jurajda 1998; Reichard et al. 2001; Oesmann 2003), although examples from American (Gale & Mohr 1978) and Nordic rivers exist (Naesje et al. 1986; Nykänen et al. 2001). The lack of studies in larger rivers is likely due to the challenges with sampling methods and general study design in large, fast-flowing river systems (Gale & Mohr 1978; Faulkner & Copp 2001; De Leeuw et al. 2007; Tomanova et al. 2013). Studies of such systems are still important, as results are not necessarily transferable between small and large river systems. The observations made of grayling larvae drift are mostly from laboratory experiments, experimental channels, or conducted in small rivers with low annual discharges. We know little about the dynamics and factors influencing the drift of grayling in larger river systems.

In this master thesis, I have studied drift of grayling fry in two neighboring, large Norwegian inland rivers. The significance of drift of grayling fry is poorly understood in Norwegian river systems, and to my knowledge there are no published studies on grayling drift from large-scale systems similar to the rivers investigated in my study. The study was designed to answer the following questions:

- Do grayling fry drift in Otta and Gudbrandsdalslågen rivers? if so;
- Are there any spatial and/or temporal patterns in the drift?
- What environmental factors influence the drift?
- Are there between-river differences in the drift patterns?

2   Study system

The study area has a large spatial scale, which is confined by upstream migration barriers in both rivers and a downstream confluence between the two rivers. The two rivers differ greatly. One is a high-gradient, fast-flowing river and the other a low-gradient, slow-flowing river. The study was conducted in the Otta and Gudbrandsdalslågen rivers located in Oppland County in Norway (Figure 1). The Gudbrandsdalslågen river (hereafter Lågen) is one of the largest rivers in southeastern Norway. It runs from Lake Lesjaskogsvatn to Lake Mjøsa, covering a catchment area of 11 567 km^2. Our study area included the 20 km river section from the rapids and waterfalls in Rosten, which is a natural upstream migration barrier (Museth et al. 2009), to the confluence with the river Otta . This section of Lågen is a slow - flowing, low- gradient river (average slope of -0.08m 100m^{-1}) (see Øistad (2014)). The river runs through Selsvollene, a large area with embankments used for agriculture. This used to be a large floodplain before embankments were built and the river channelized (Thorsnæs 2009). The water velocity is relatively low, and the substrate dominated by sand and gravel. At the town Otta, - the substrate in Lågen becomes coarser (i.e. more gravel and stones), and the gradient and the water velocity higher than in the upstream section. At the hydrological station in the Rosten waterfalls, the mean annual discharge is 32.7 m^3/s (Oppland Energi 2009). The river is characterized by spring floods in May, June and July, fed by snowmelt in high-altitude mountain areas. The traditional flood peak is in the end of May to early June, with an average flood discharge of 311 m^3/s and the highest recorded flood discharge in Rosten of 627 m^3/s (Drageset 2000). There are several known spawning sites for grayling in Lågen within this study area (Museth et al. 2009). The largest is found at Fevollen/Grenet, downstream the Rosten rapids, 13 km upstream the confluence with Otta river.

Otta river is the largest tributary to Lågen, and runs from Lake Djupvatnet in Møre og Romsdal County all the way to the town Otta (135 km) in Oppland County, where it meets Lågen river (Store Norske Leksikon 2009). The catchment of Otta is 4150 km^2, which is twice the size of Lågens catchment upstream of the confluence (Museth et al. 2011). The river system of Otta has several hydropower reservoirs before running through Eidefoss-powerplant which has an annual mean discharge of 111 m^3/s (Museth et al. 2011). During winter, the discharge in Otta is increased compared to its natural state due to release of water

from the reservoirs. During spring and summer the discharge is reduced due to filling of the reservoirs. Otta river is glacier fed, and the natural discharge increases rapidly due to snowmelt and glacier runoff in June and July (Drageset 2000). The yearly floods occur in June, July and August, with average peaks in the start of June and mid-July (Drageset 2000). The average flood discharge in Otta is 650 m^3/s, while the largest discharge measured during floods is 1387 m^3/s (Drageset 2000). Since Otta drains the high altitude mountain area Jotunheimen, with glaciers, more snow and a later snowmelt than the mountain areas draining to Lågen, the timing of floods in Otta may arrive both at the same time, and often after the flood in Lågen (Drageset 2000). The study area in Otta River includes the 15 km river section from the Eidefoss Dam to the confluence with Lågen River. The Eidefoss powerplant was built utilizing a natural waterfall considered to be a natural migration barrier even before dam construction (Huitfeldt-Kaas 1918). In this area, the largest known spawning area for grayling is located just downstream the Eidefoss Dam, but there are several known spawning areas for grayling further downstream (Museth et al. 2011). Otta River is a fast-flowing, high-gradient river (Average slope -0,31 m per 100 m within this study area (Øistad 2014)). There are several small rapids and deep pools and the substrate varies between rocks and boulders with some gravel in some of the more slow flowing pools (Kraabøl et al. 2007).
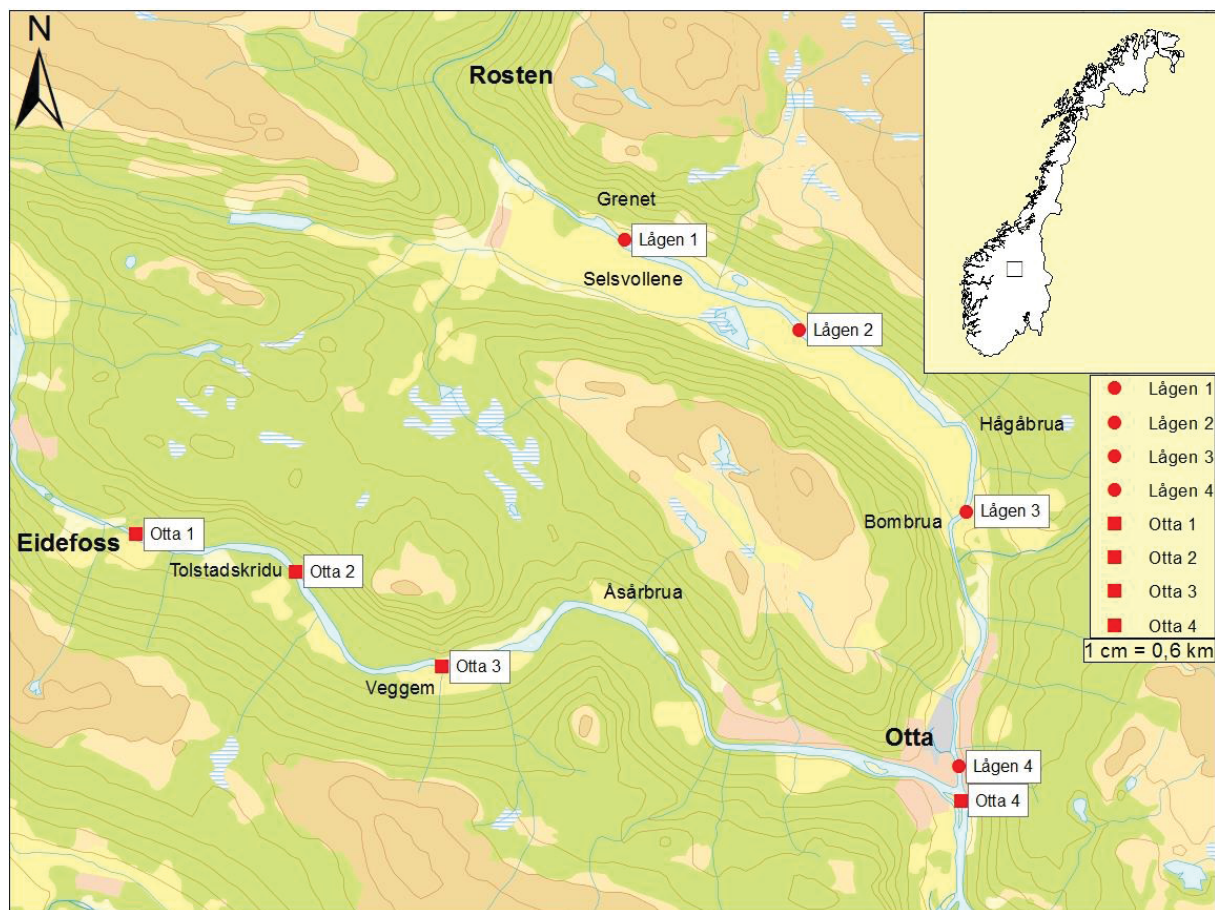
Figure 1: Study area and drift trapping stations in Otta and Gudbrandsdalslågen rivers, Oppland County, Norway.

The temperature difference between these rivers shifts several times a year. In spring and autumn, Otta River is warmer than Lågen River, while it is colder during summer due to snowmelt in the Jotunheimen mountain areas. Museth et al. (2011) recorded 2.2-4.1 °C higher temperatures in Otta River than in Lågen River during September – November in 2008 and 2009. In April and May, the mean differences was 1.3-1.7 °C, with Otta River being the warmer, most likely because of release of warmer water from the large hydropower reservoirs.

2.1 The grayling

In the Otta and Lågen rivers, brown trout and grayling are the dominant fish species. The present study includes grayling only. Compared with the strong population decrease of

grayling in many countries in Europe, due to habitat fragmentation, overfishing and pollution (Northcote 1995), the grayling population in this study system is still very viable (Kraabøl et al. 2007; Museth et al. 2011). The grayling is a freshwater fish in the salmonid family, recognizable by its large dorsal fin (Pethon & Nystrøm 1985). It is mostly found in rivers, but also inhabits some lakes (Pethon & Nystrøm 1985). The grayling is a spring spawner (Janković 1964; Bardonnet et al. 1993; Northcote 1995). Bardonnet and Gaudin (1991) reported that the eggs hatch after 276-320 degree days, while d'Hulstere and Philippart (1982) reported 177 degree days. However, there may be significant differences in development time between populations (Haugen 2000a). The spawning period for grayling in the study area was estimated to be between May 25 and June 15 in 2008 (Museth et al. 2009). In this system, the grayling sexually mature at age 5 (Museth et al. 2009). The grayling has small eggs and a high fecundity (Janković 1964; Penaz 1975; Northcote 1995), though it is known to vary between populations (Haugen 2000b). Grayling do not make redds as most other salmonids do, but the female deposits her eggs a few cm under the gravel surface by pressing her genital opening, with the aid of peduncle cross-over from the male, down into the substrate during spawning (Fabricius & Gustafson 1955). The eggs are deposited in the gravel, becoming lodged in the substrate (Northcote 1995). There they remain close to the surface of the substrate until hatching (Fabricius & Gustafson 1955). The grayling spawn in shallow parts of running rivers compared with other salmonids (Fabricius & Gustafson 1955), and the species also prefers finer substrate on the spawning grounds than trout and salmon (Fabricius & Gustafson 1955; Northcote 1995; Nykänen 2004).

After hatching, the grayling fry makes a downward movement into the substrate (d'Hulstere & Philippart 1982). The fry spends several days in the substrate before emerging (Kratt & Smith 1977; d'Hulstere & Philippart 1982; Scott 1985; Bardonnet & Gaudin 1990a). Scott (1985) reported a 4-5 days period between hatching and emergence. Kratt and Smith (1977) observed 3-4 days, while Bardonnet and Gaudin (1990a) observed a 7-8 days period. The grayling fry's photoreaction switches from negative to positive or neutral some days after hatching (Penaz 1975; Pavlov 1994), and thereafter they emerge from the gravel. While other salmonid species fry seem to be photonegative (Woodhead 1957; Gustafson-Marjanen & Dowse 1983), light seems to promote emergence in grayling fry (Bardonnet & Gaudin 1990a). From aquarium studies it has been shown that grayling fry emergence peaks at the start and end of night (Bardonnet & Gaudin 1991). Peaks, both during dusk and dawn, have also been documented

under natural conditions (Bardonnet & Gaudin 1990b; Bardonnet et al. 1991; Grimardias et al. 2012). This differs from other salmonids which mainly are nocturnal (Gustafson-Marjanen & Dowse 1983).

3   Materials and methods

To catch grayling fry, I mounted drift traps and checked them at least every 24h over a period of 21 days. The study period lasted from June 17 to July 7 when glacier-fed flooding in Otta made the handling of traps impossible. To study the difference between the high - gradient Otta and the low - gradient Lågen, four stations with three traps each, were mounted in both rivers (Figure 1). Station 1, the furthest upstream, was placed directly downstream of known grayling spawning sites in both rivers, with known migration barriers right upstream. Stations 2 and 3 in both rivers were placed with relatively similar distances downstream from the first station, with no known spawning sites in between. The fourth station in both rivers were placed downstream of new spawning sites, close to the confluence between the two rivers, to assess whether the fry reached the confluence and attempt to quantify the amount of fry contributed by each river.

3.1   Drift trapping

To capture the drifting grayling fry, drift traps were made similar to those used by Bardonnet et al. (1991) and Grimardias et al. (2012). The frames were made from a plastic pipe with 16cm diameter cut into short tubes. The net (1mm mesh size) was glued together and attached to the frame, making a slightly conical shape with a length of 1m. Two holes were drilled into the trap frames to allow it to slide onto rebar fitted into the riverbed substrate. Zip-ties were used to regulate each traps vertical position on the bar in the river. Each bar held three traps. The deepest trap rested on the riverbed, along the substrate, the second one was placed at a mid-position relative to the water depth (approximately 25-50 cm depth) and the third just below the surface (Figure 2). For security and practical reasons all stations were placed close to the bank, and none mid-channel. From June 25 to July 4 some of the traps were checked every 12 hours to investigate the diel pattern in the drift of fry (Figure 3). Every time the traps

were checked, the content was flushed into a white bucket to ease the sorting of the contents. The fry's total length was measured, and then put on vials with 95 % alcohol (Figure 4). Every trap was flushed with water and visually checked to make sure no fry was left behind, before placing the traps back on the rebar in the river. Water velocity was measured directly in front of each trap every 24 h with a pygmy water speed meter (AquaCount from JBS Instruments). Because of differences in discharge through the study period, some of the traps had to be adjusted in height, and some had to be moved (the furthest approximately 15 m from its original position).

Figure 2: One station with 3 drift traps in use in Lågen June 17- July 7 2014. Photo: Casper van Leeuwen.
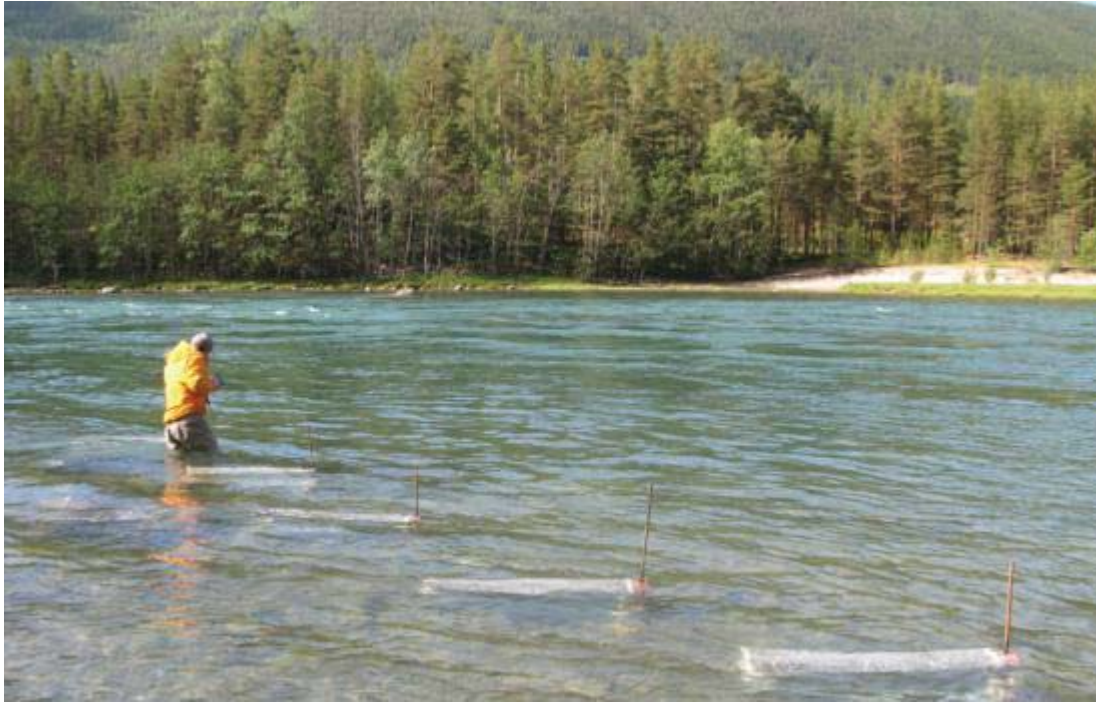
Figure 3: Checking the traps at station 2 in Otta. Photo: Casper van Leeuwen.

b)

Figure 4: a) Grayling fry captured by drift trapping in Otta July 2014. Photo: Casper van Leeuwen. b) Slightly more developed grayling fry, captured late in the study period in Lågen 2014. Photo: Casper van Leeuwen.

In Otta, the station furthest upstream (Otta 1) was placed directly downstream of the Eidefoss Dam. Station 2 in Otta (Otta 2) was placed 3.3 km further downstream at Tolstadskridu. Station 3 (Otta 3) was located 2.7 km downstream of station 2, near Veggem. Station 4 (Otta 4) was located 9.2 km downstream of station 3, just downstream of the confluence. This was possible because Otta and Lågen do not mix until several hundred meters downstream of the confluence. In Lågen, the station furthest upstream (Lågen 1) was placed at Grenet, directly

downstream from a known spawning site for grayling. The second station (Lågen 2) was along Selsvollene, 2 km downstream from Lågen 1. The third station in Lågen (Lågen 3) was placed 5.9 km downstream from Lågen 2, just upstream of Bombrua. The fourth station in Lågen (Lågen 4) was placed 4.2 km downstream of Lågen 3, under the bridge in the town Otta, near the confluence with River Otta.

The initial setup included four stations in each river, with a total of 24 traps. This setup was adjusted during the study period (Table 3). After the first day with catches of drifting fry, two more rebars with a total of 6 traps was supplemented to station 1 in Otta on June 26 (Lågen 1.2 and Lågen 1.3). These traps were also checked every 6 hours until June 30 to investigate possible diel patterns in the drift. On June 30, the two extra rebars with a total of 6 traps were moved to station 1 in Lågen, to get more data on the diel pattern of the drift. At this time there were low catches in station 1 in Otta and better catches in Lågen 1. The traps at this station were checked every 12 hour to differentiate between daytime and nighttime drift. After checking the traps in station 2 and 3 in Lågen and station 1 and 3 in Otta on July 2, the traps were moved and the 4 rebars with a total of 12 traps were supplemented to station 2 in Otta. The intention was to move the traps to stations where I captured more fry, to increase the amount of data on fry length, drift depth, diel drift patterns and the duration of the drift period. The trapping ended before the fry ceased to drift, when a glacier-fed flood made handling of traps impossible.

3.1.1 Pilot study

In 2013, a pilot-study with a simpler sampling design was conducted. Two stations were made in each river. One downstream of a spawning area and one near the confluence in both rivers. In Otta, the upstream station was placed at Tolstadskridu (station Otta2 in 2014) and the downstream station just below the confluence (Otta4 in 2014) (Figure 1). In Lågen, the upstream station was placed at Grenet, just upstream of station Lågen1 in 2014. The downstream station in Lågen was placed near the confluence between the rivers, close to the station Lågen 4 in 2014 (Figure 1). Two traps were mounted at each station (a total of 8 traps) with zip-ties attaching them to rebar fitted into the substrate. The traps were checked daily from June 13 to July 13, and the grayling larvae counted. A flood during June 22 – 24 washed

away some of the traps and made it impossible to check some of the stations. Drift traps were moved between stations to replace lost traps.

3.1.2 Temperature and discharge

Daily temperature data and daily averages of discharge from monitoring stations just upstream of Eidefoss (Station No. 2.25.0.1001.0 Lalm and Station No. 2.674.0.1003.3 Otta v/Eidefoss kraftstasjon), Rosten (Station No. 2.614.0.1001.0 Rosten) and a station in Lågen just upstream of the confluence with Otta (Station No. 2.653.0.1003.3 Lågen ovf. Otta) was provided by the Norwegian Water Resources and Energy Directorate.

3.2 Data analyses

3.2.1 Environmental factors influencing drift

In order to model the influence of external environmental factors (water temperature, discharge, water velocity), time and drift distances on trap catches a zero-inflated Poisson (ZIP) modelling approach was used (Lambert 1992; Zuur et al. 2012). ZIP models explicitly model factors affecting zero-observations as a probability process (i.e., logit-linked generalized linear models, GLM) and non-zero observations as a Poisson process (i.e., log-linked GLM). Hence, ZIP models include two submodels where the count data are made conditional on the probability of not observing zero values. Other potential modelling approaches, such as negative binomial and ordinary Poisson models were compared to the ZIP alternative, all fitted with a river*time^2 prediction structure, performing Vuong tests (Vuong 1989). The ZIP approach always came out as superior in these tests ($p<0.0001$). The applied ZIP approach produced the following likelihood function (i.e., the likelihood of a single observation):

$$l(y|\mathbf{x},\mathbf{z},\boldsymbol{\beta},\boldsymbol{\gamma}) = P(\mathbf{z'}\boldsymbol{\gamma})I(y=0) + \{1-P(z'\boldsymbol{\gamma})\}f(y|\mathbf{x'}\boldsymbol{\beta})$$

, where $\mathbf{z}$ represents the vector of zero-observation covariates and $\boldsymbol{\gamma}$ the corresponding coefficients; $\mathbf{x}$ is the count covariate vector and the $\boldsymbol{\beta}$s the corresponding coefficients. P represents the cumulative distribution function fitted to specify the $y>0$ outcome and f is the probability mass function corresponding to the count model (here the Poisson distribution).

In order to separate true drifting dynamics from dependencies arising from the spatial- and repeated measurement structure embedded in the sampling design I included random factors in the Poisson part of the model. The random factors reflected the sampling design where trap ID was nested under station, which again was nested under river. The same random effect model structure was used in all models. As the resulting mixed effects ZIP modelling approach is not included in the most used ZIP-packages in R, a recently developed script developed by Ben Bolker, named ZIPme (downloadable from: https://groups.nceas.ucsb.edu/non-linear-modeling/projects/owls/R/owls_R_funs.R), was used.

Model selection was undertaken by using Akaike's Information Criterion (AIC) and after finding the most supported predictor variables to include in the model, backwards selection was undertaken to find the detailed models structure (sensu Zuur et al. (2009)). Motivated by recommendations in the mark-recapture modelling literature (e.g., Lebreton et al. (1992)), model selection was performed in two steps where the capture process, which was considered to be reflected by the zero-inflation model, was modeled prior to the count data modelling. The most supported zero-inflation model structure was sought by fitting candidate models under a fully factorial time-by-river count model part (and the mentioned random effects model structure). The time effect was here modelled as a second-degree polynomial in order to allow for a catch peak during the course of the drifting period. After establishing the most supported zero-inflation model structure, the previously described model selection route was followed for the Poisson model part.

3.2.2 Drift distances

Predicted drift distances from emerging grayling fry from each night "cohort" was estimated. To estimate the drift distances I assumed only passive nighttime drift. Sunrise and sunset times were calculated in R using the suncalc function in the RAtmosphere package. The times for sunrise and sunset was assumed to be the same in the whole study area, using the confluence between the rivers as a fixed position in the suncalc function. The cumulative distance traveled by each nights "cohort" was calculated by the water velocity measured at the nearest station. The measured water velocities (m/s) x 3.6 x night length (h) gave the drift length in kilometers and was added up during the observed drift period to get cumulated drift

distances. In cases of missing values for water velocity, a linear regression between water velocity and discharge was used to estimate water velocity for stations where this relationship was significant ($p<0.05$).

3.2.3 Between river difference in fry size

The size of drifting fry was compared between rivers using ordinary least-square linear models as available from the lm-procedure in R. This was done by fitting linear models, testing river and day effects on total length of caught drifting grayling fry in Otta and Lågen.

4   Results

Drifting grayling fry were documented in both rivers. In the period June 17-24 no drifting grayling fry were captured. June 25 was the first day with catches in Otta and July 6 the last. In Lågen, June 27 was the first day with catches of grayling, while July 7 was the last (Figure 5). There was large variation in the number of caught fry both between rivers and stations within each river. Most grayling fry were caught in Otta, with fry captured at all stations in the river, particularly in the traps at station Otta 2. A peak in the drift in Otta was observed on July 1, six days after the first drifting fry was recorded. In Lågen, grayling fry was caught at the stations Lågen1 and Lågen4. No fry was captured in the slow flowing section along Selsvollene (stations Lågen2 and Lågen3), but some grayling larvae were observed along the banks. Although no clear peak in the drift was observed in Lågen, the maximum number of grayling captured was on July 1, the same date as in Otta.
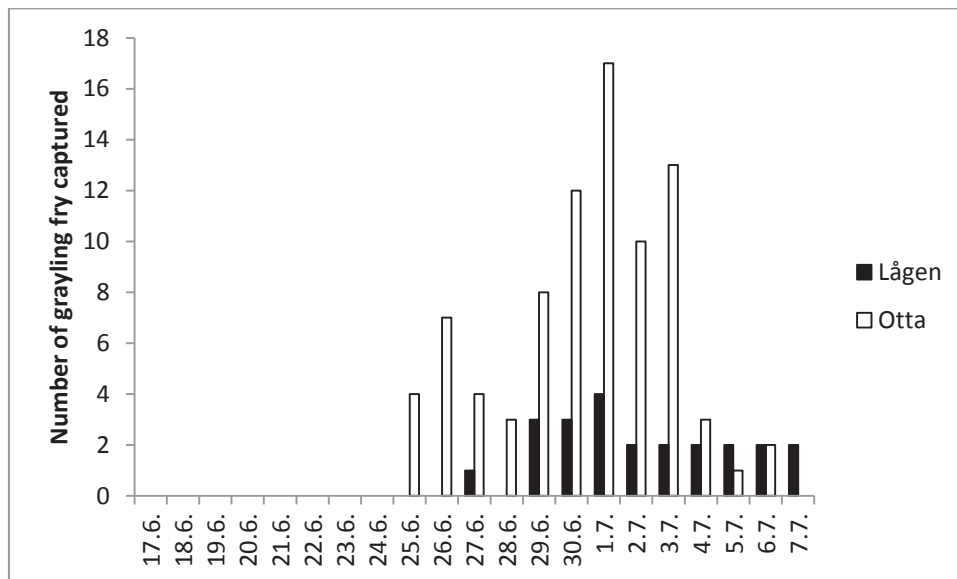
Figure 5: Number of grayling fry captured by drift traps in the river Otta and Lågen June 17 – July 7 2014.

A diel pattern in the drift was observed, with the largest proportion of the drift occurring during night (Figure 6). During the 12 hour sampling period, 20 fry were captured during night sampling, while three fry were captured during daytime sampling. No fry was captured during the six hour sampling period.
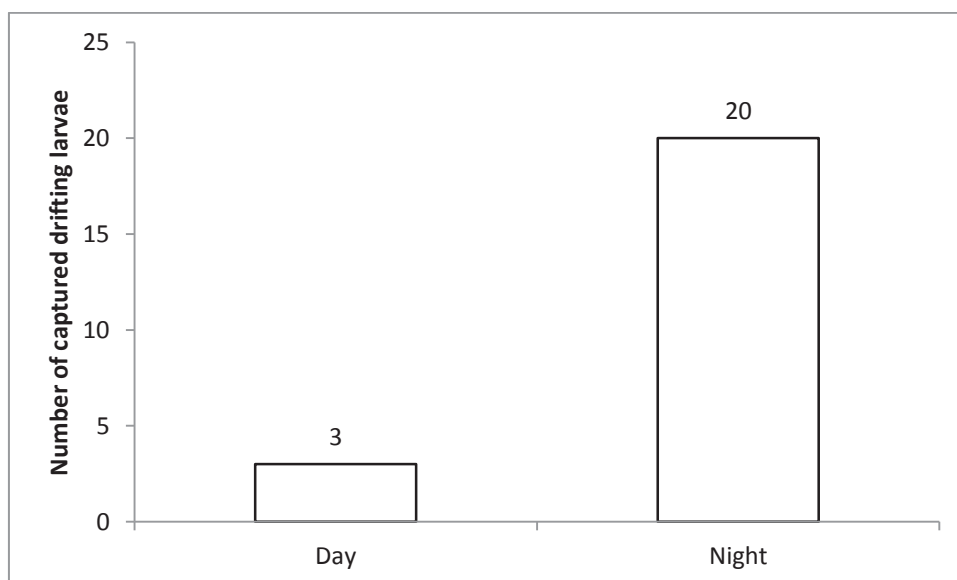
Figure 6: Number of drifting grayling fry captured during daytime and nighttime trapping in Otta and Lågen June 27- July 7 2014.

The total number of grayling fry captured in drift traps in both rivers was higher in the middle and deeper parts of the water column than close to the surface (Figure 7).
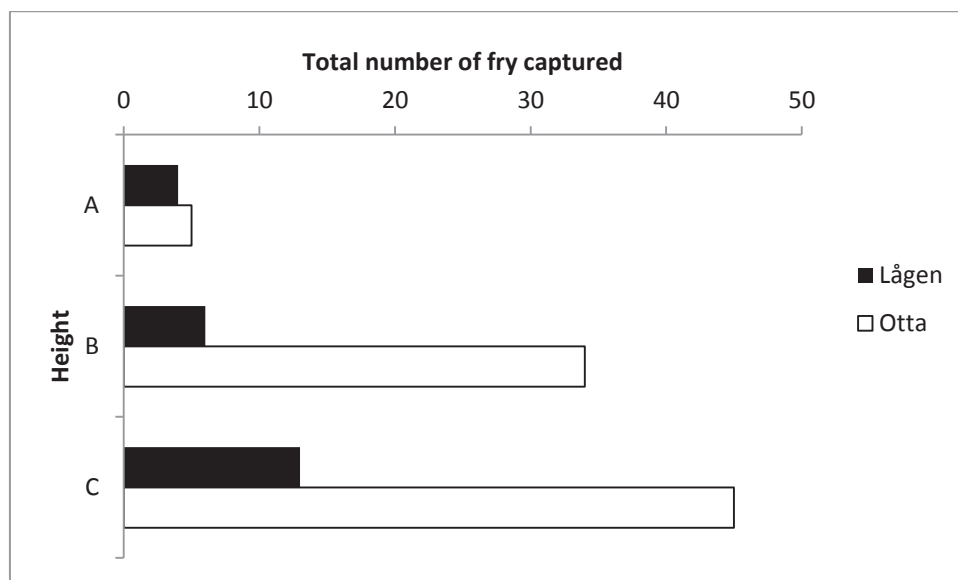
Figure 7: Total number of grayling captured by traps at different height in the water column. a) close to surface, b) mid position relative to water depth and c) close to bottom substrate in the rivers Lågen and Otta June 25 – July 7 2014.

Using estimated night-drift distances the grayling larvae in Lågen was assumed to reach known nursing areas downstream of the confluence with Otta within 3-4 days (Figure 8). After 2-3 days with passive nighttime drift the grayling larvae in Otta is assumed to reach the same nursery area (Figure 9).
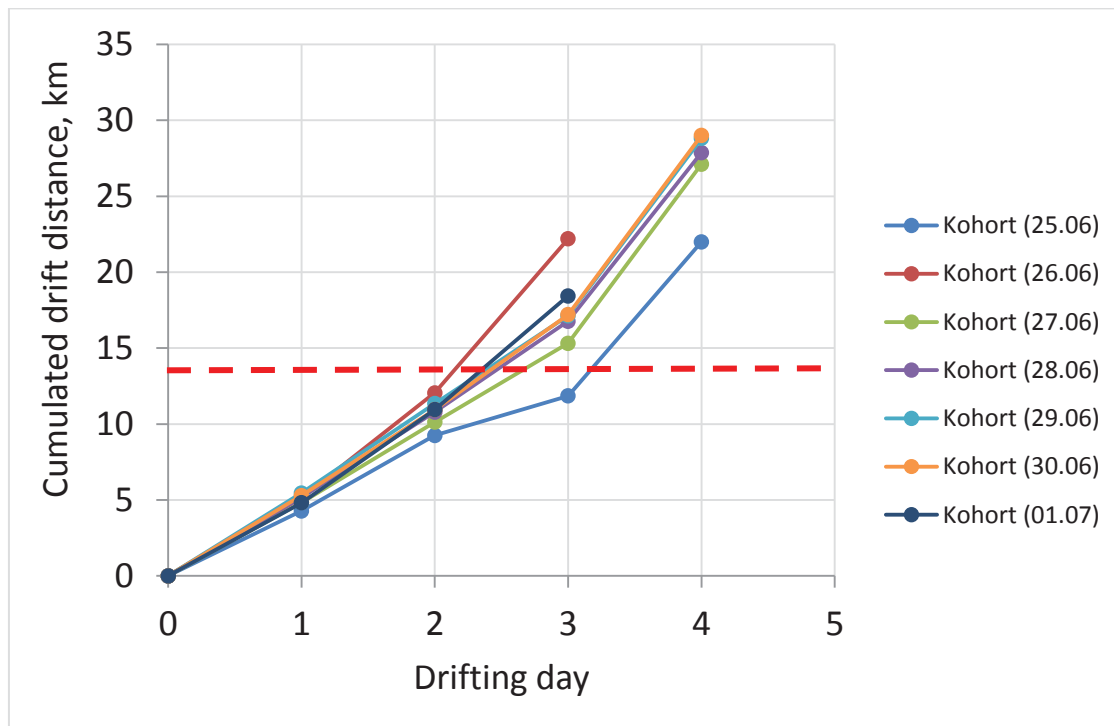
Figure 8: Cumulated drift distances of grayling fry emerging at different dates in River Lågen 2014. Dashed line indicating distance to a known nursery area upstream of Bredebygden.
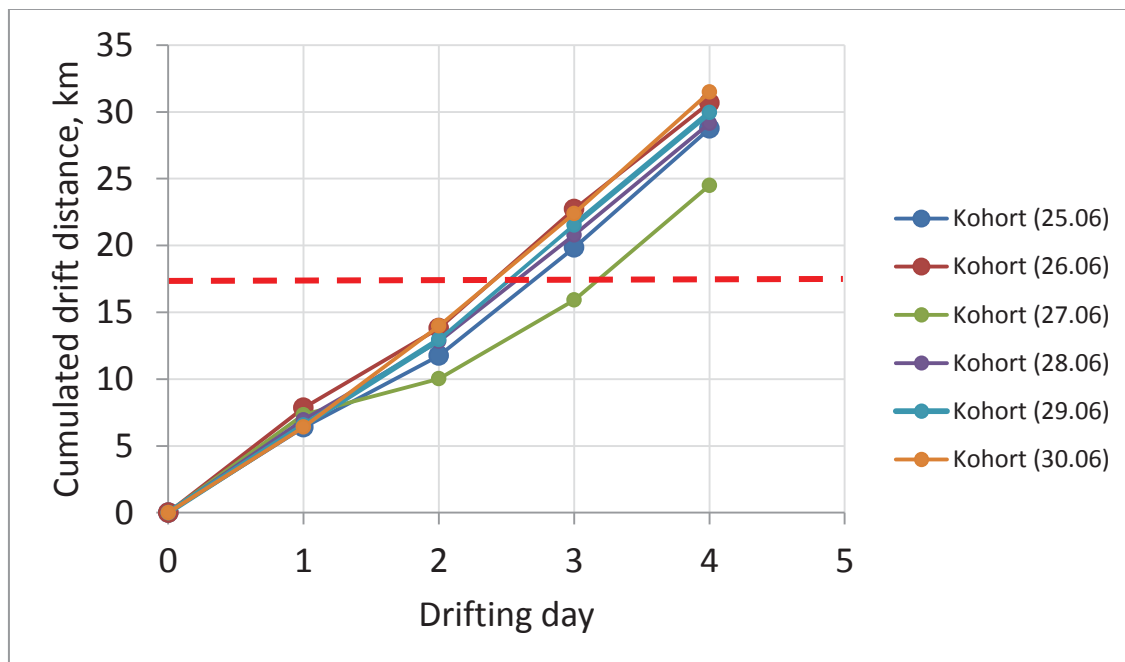
Figure 9: Cumulated drift distances of grayling fry emerging at different dates in River Otta 2014. Dashed line indicating distance to a known nursery area upstream of Bredebygden.

The grayling fry caught during the study period in 2014 differed in size, with the smallest being 14 mm, and the largest 21mm total length (Figure 10). The average size of drifting grayling larvae was 16.0 ± 1.3 mm (SD). The largest larva was caught late in the study period in Lågen. It had absorbed the yolk sack, and had more developed pigment and fins than the smaller fry caught earlier in the study period.
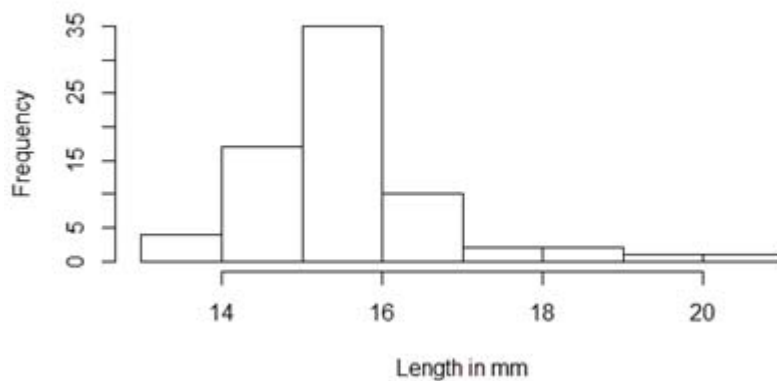
Figure 10: Length distribution of grayling fry captured in the rivers Otta and Lågen June 25 – July 7 2014.

There was a significant interaction between the day number in the study period and river effects on the observed length in the grayling fry (p<0.0001) (Table 1). While the fry in Otta showed no clear development in length during the study period, the fry captured in Lågen showed a significant increase in total length during the study period (Figure 11).

Table 1: Parameter estimates and corresponding ANOVA test statistics for the linear model testing river and day effects on total length of caught drifting grayling fry in Otta and Gudbrandsdalslågen June 25- July 7 2014. R^2_{adj} = 0.2653.

Parameter estimates					
	Estimate	SE	p		
Intercept [Lågen]	13.34888	0.73466	< 2e-16		
Day	0.38337	0.08300	1.77e-05		
River [Otta]	2.82681	0.80427	0.000788		
Day*River[Otta]	-0.44126	0.09741	2.45e-05		
ANOVA test					
Effect		df	SS	MSS	F	p
Day		1	6.082	6.0821	5.1169	0.02689
River		1	3.575	3.5754	3.0080	0.08739
Day*River		1	24.390	24.3899	20.5192	2.449e-05
Residuals	68	80.828	1.1886		
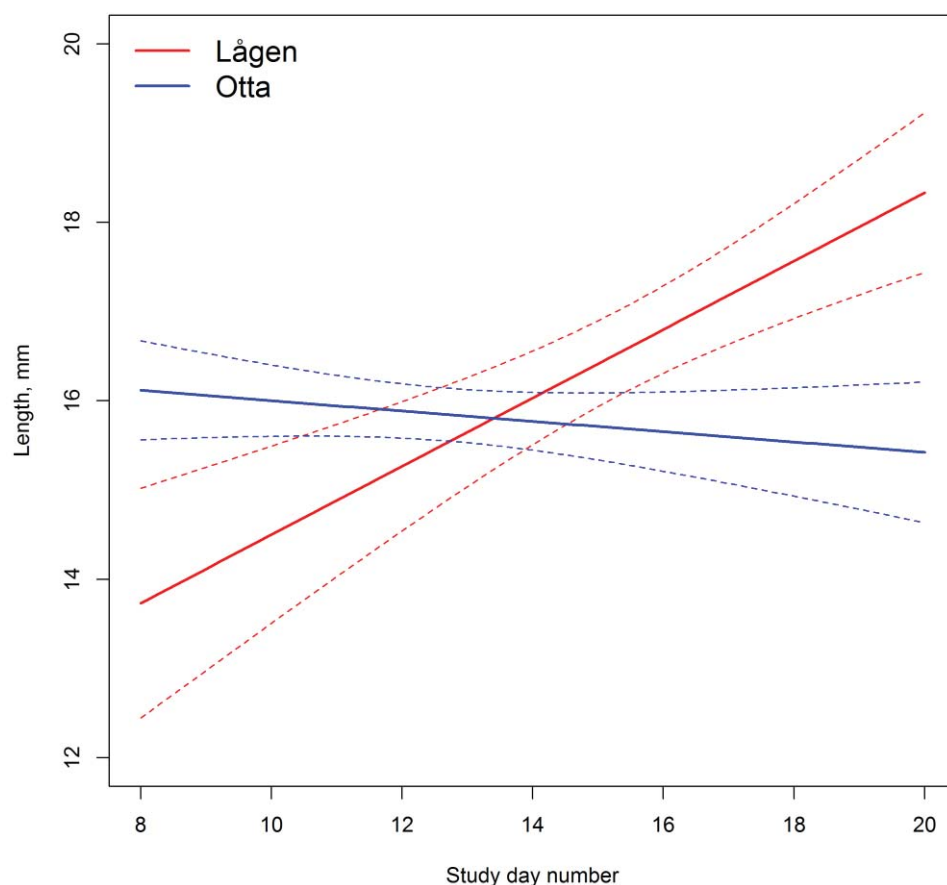
Figure 11: Predicted total length of grayling fry captured in drift traps in Gudbrandsdalslågen and Otta June 25- July 7 2014 with 95% confidence intervals (dashed lines). Predictions were estimated from the model provided in Table 1.

The discharge patterns were different between the years 2013 and 2014. In 2013, there was a peak in the discharge in both Otta and Lågen 2-3 days before the grayling fry started drifting (Figure 12). During the same period in 2014 discharge was declining (Figure 13). The water discharge was lower in both rivers during the course of the drift in 2014 compared with 2013. The number of grayling fry captured per trap day was higher in 2013 than 2014, while the timing of the drift was the same in both years, with the first grayling caught in drift traps June 25 in 2014 and June 26 in 2013. The duration of the drift was also similar between the two years, where drift was recorded over a period of 12 days in 2013 and 13 days in 2014.
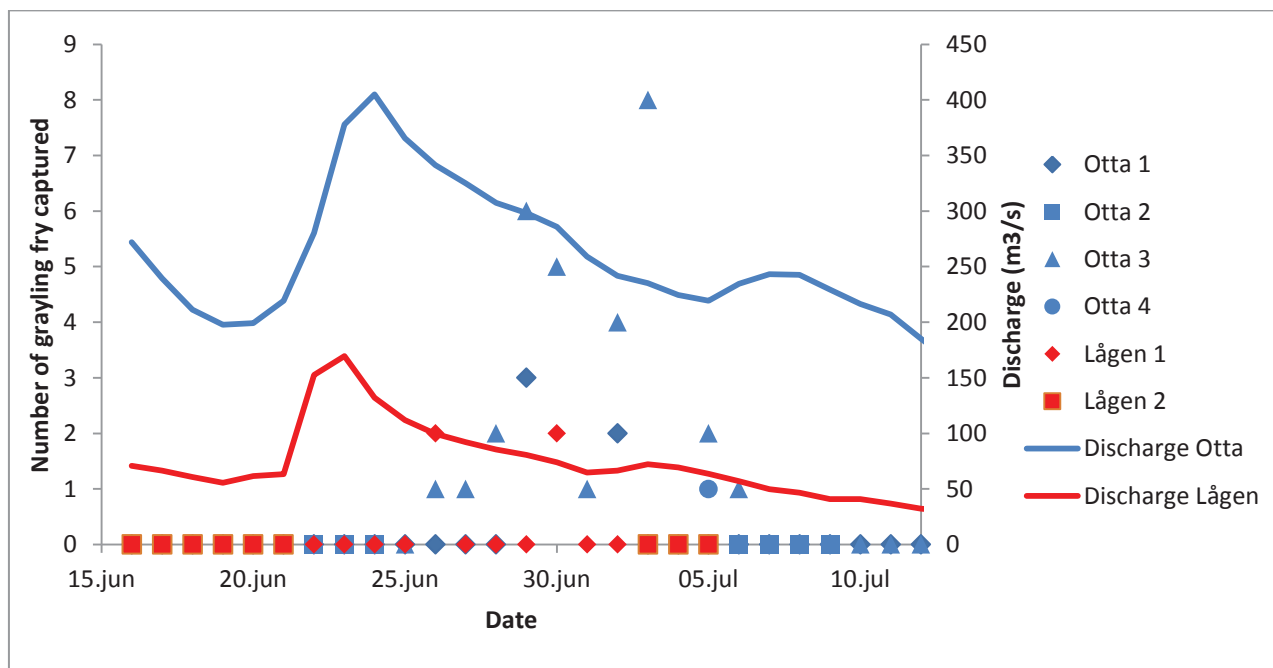
Figure 12: Number of grayling captured by drift traps, and daily discharge in the rivers Otta and Lågen, June 15-July 13 2013.
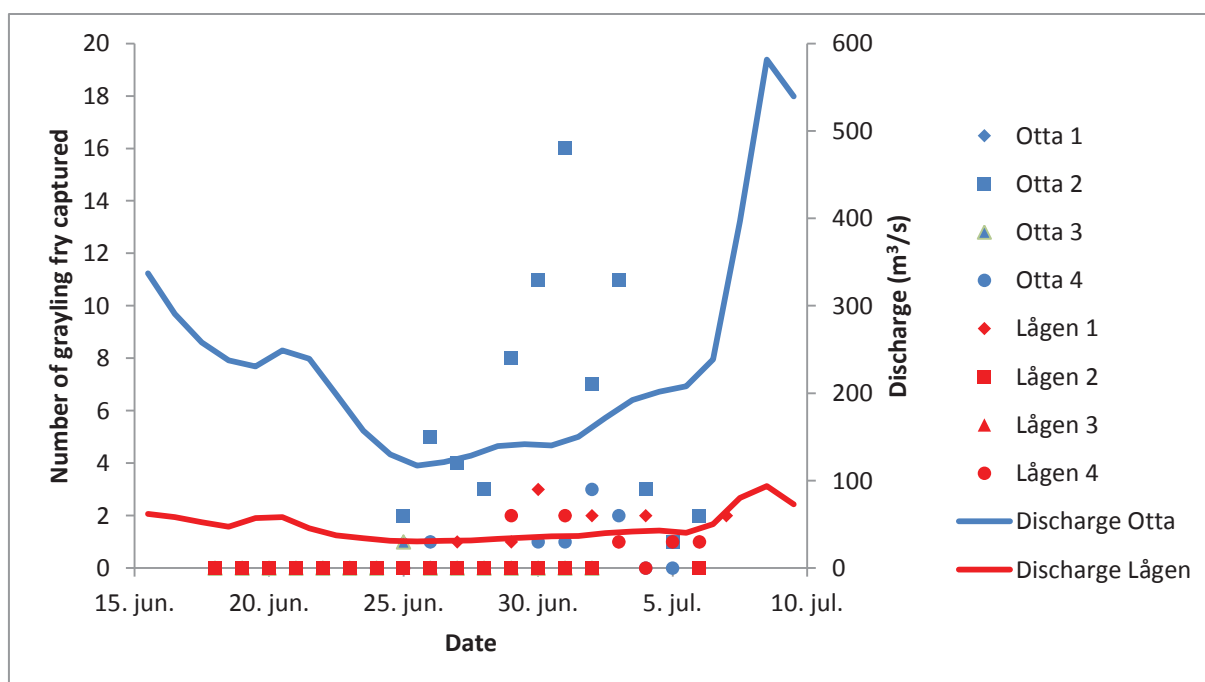
Figure 13: Number of grayling captured by drift traps, and daily discharge in the rivers Otta and Lågen, June 15-July 13 2014.

Table 2: AIC table for the ten most supported Zero- models in the ZIP-me models of grayling fry drift in Otta and Lågen in 2014. For the selection process the count- model was fixed with the variables river*day^2. ΔAIC= deviation relative to the most supported model. See appendix for complete model selection table (Table A2).

Zero-model	AIC	ΔAIC
River site + Height	329.4	0
River site	339.9	10.5
Height	341.2	11.8
Ln distance to spawning area	344.8	15.4
River	344.9	15.5
Standardized discharge	345.1	15.7
Water temperature	345.5	16.1
Distance to spawning area	345.5	16.1
Water velocity	345.5	16.1
Water velocity^2	346.2	16.8

Table 3: AIC model selection table for the ten most supported count-models from the ZIP models of grayling fry drift in Otta and Lågen in 2014. For the selection process, the most supported zero-model was used (River site + Height). ΔAIC= deviation relative to the most supported model. See appendix for complete model selection table (Table A3).

Count-model	AIC	ΔAIC
Degree days^2 * River	324.9	0
River + day^2	329.2	4.3
River * day^2	329.4	4.5
Standardized discharge + day^2	329.8	4.9
Day^2	330.8	5.9
Water velocity^2 + day^2	331.3	6.4
Water velocity + day^2	332.3	7.3
Distance to spawning area + day^2	332.7	7.8
Water velocity * day^2	333.8	8.9
Degree days^2 * Standardized discharge	333.9	9.0

Different environmental variables were modelled in order to see which factors could explain the observed drift pattern in 2014. The second-degree polynomial of number of degree days (over 5 °C) as a continuous variable and river as a factorial model best explained the observed pattern in the drift.

Table 4: Parameter estimates for with fixed and random effects for the most supported ZIP-me model using river site and height as variables for the zero- inflation model with degree days (°D) over 5°C and river as factors in the count model. Modelling number of caught grayling fry per trap per day in Otta and Gudbrandsdalslågen June 25 – July 7 2014.

Submodel	Fixed/Random	Effects/terms	Estimate	SE	z	p
Zero-inflation	Fixed					
		Intercept [Lågen1]	6.1904	3.9667	1.561	0.11862
		River site [Lågen2]	6.9763	2.5909	2.693	0.00709
		River site [Lågen3]	6.9763	2.5909	2.693	0.00709
		River site [Lågen4]	-6.9738	4.0166	-1.736	0.08252
		River site [Otta1]	4.2034	0.7928	5.302	1.15e-07
		River site [Otta2]	-6.8030	3.9870	-1.706	0.08795
		River site [Otta3]	4.3017	0.9764	4.406	1.05e-05
		River site [Otta4]	0.5014	0.8258	0.607	0.54373
		Height [B]	-8.6880	3.9942	-2.175	0.02962
		Height [C]	-8.4054	3.9889	-2.107	0.03510
Count	Fixed					
		Intercept	5.27E+01	2.64E+01	-1.991	0.0464
		Degree days	5.12E-01	2.67E-01	1.915	0.0555
		Degree days^2	-1.27E-03	6.73E-04	-1.889	0.0589
		River[Otta]	9.53E+00	2.93E+01	-0.326	0.7445
		Degree days[Otta]	2.00E-01	3.03E-01	0.66	0.5094
		Degree days^2[Otta]	-7.64E-04	7.87E-04	-0.972	0.3312
	Random					
		Trap ID:(Site:River)	6.77E-01	8.23E-01		
		Site:River	2.22E-09	4.72E-05		
		River	5.50E-10	2.34E-05		

The model best predicting the number of captured grayling larvae included the two variables river and degree days over 5 °C, including a zero-model structure with river-site and height as variables (Table 1&2). The best fitted model shows a difference in the number of degree days (°D) before drift between the rivers in 2014 (Table 3). While the drift of grayling fry is modelled to peak at 175°D in Otta, it peaks at 200°D in Lågen (Figure 14). It also shows the predicted numbers of grayling caught at the different stations are generally higher in Otta than in Lågen. While there is predicted drift over the whole river section in Otta, there is no predicted drift in the slow flowing sections of Lågen (Figure 14).

In 2013, the drift in Otta peaked after 177.5 degree days (over 5 °C), while it peaked after 179.2 degree days in 2014. The drift in Lågen showed no peak in 2013, but the drifting grayling larvae were caught between 143 and 166 degree days, while the drift in Lågen peaked after 197.3 degree days in 2014 (Figure 14). The timing of the drift explained by degree days stayed the same in Otta between 2013 and 2014 and there was large variation between years in Lågen.
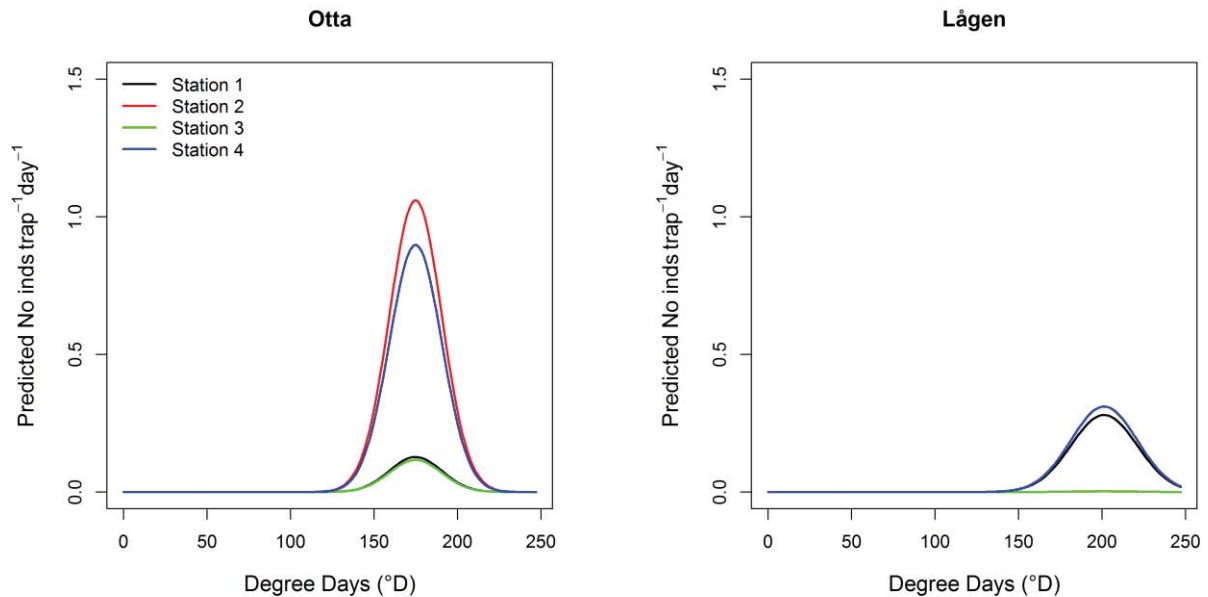

Figure 14: Predicted number of grayling fry captured each day at each station by drift trapping with traps along the substrate as an effect of degree days over 5 °C in the rivers Otta and Lågen. Predictions were estimated from the most supported ZIPme-model provided in Table 4.

5   Discussion

This study has documented drift of grayling fry in two large inland rivers in Norway. Both spatial and temporal patterns in the drift were observed. The grayling fry drifted over a short time period in June-July, deep in the water column and mainly at night, however, with between-river differences in the spatial pattern of the drift, with fry in Otta drifting through the whole river section while the drift was limited to the upper and lower reaches in Lågen.

5.1   Temporal patterns in drift of fry

Although drift trapping in 2014 ended before the drift ceased, the number of captured drifting larvae was declining at the end of the study period, possibly indicating the drift period was approaching its end. The observations from the pilot study in 2013 also showed a short drift period, with catches over an 11- day period. The temporal pattern in drifting grayling fry observed in this study is similar to observations in English, French and Swiss rivers (Scott 1985; Bardonnet et al. 1991; Grimardias et al. 2012), and confirms a short drift period of grayling also in larger Nordic river systems. There are reports of longer drift periods of grayling fry, but these are generally from rivers with low discharges and with nursery areas close to the emergence site. Grimardias et al. (2012) captured drifting grayling fry from the middle of April to the start of June. The abundances of drifting grayling larvae decreased after the first week of sampling, although a longer drift period was observed. The studied river had a low discharge ($2.51 \ m^3/s$), possibly explaining the long drift period. The observed longevity of the drift period could also be related to the large difference in altitude along these southern rivers. The earlier spring and thus also spawning in southern Europe compared to northern rivers can explain the earlier start of the drift period. A similar pattern, with a longer drift period downstream a slow-flowing tributary with good nursery habitat was observed by Bardonnet et al. (1991). Haddeland (2012) captured drifting grayling fry in a small, slow-flowing tributary to Lesjaskogvatnet during a period of three weeks, with a clear peak in number of captured fry July 9-10, illustrating the effect of flow on the duration of the drift period in a northern river. All grayling fry emerged during a 10 day period in an experiment in a tributary to the River Rhone in France (Bardonnet & Gaudin 1990b). Scott (1985)

observed grayling emergence over a 10-12 day period in an English river, while Haugen (2000a) observed a 3-5 day period of emergence in several populations in Norway. Although grayling fry can rest at the gravel bed after emergence until nightfall in low current velocities, they drift within a short period after emergence (Bardonnet & Gaudin 1990b; Grimardias et al. 2012). A short emergence period will therefore likely lead to a short period of first displacement of grayling fry (Pavlov 1994). The first drift of grayling fry from spawning areas to the first feeding habitats seems to take place over a short time period, dependent on variations in discharge and water velocity. This may be explained as an adaptation to predation, where the total loss to predation on the population level is smaller when the concentration of drifting larvae is high during a short drift period (Peterman & Gatto 1978; Smith 1985).

The timing of the drift of grayling fry was remarkably similar in 2013 and 2014, despite a large variation in the discharge before and during the drift period between the years. This may demonstrate that the grayling fry must cope with widely different conditions after emergence in different years. Though the timing of drift of grayling in this river system seems similar between years, the timing in relation to floods will likely vary greatly between years, as I observed in 2013 and 2014. In some years the grayling fry will emerge during floods and other years during low-flow periods, possibly having a great influence on the longitudinal distribution of drifting grayling larvae (Harvey 1987). This might be the reason behind the dynamic use of the river system observed in adult grayling followed by telemetry in this river system (Junge et al. 2014).

There are few studies investigating patterns of fish drift with durations over several years. Abundance of drifting fry in other taxa is known to vary between years, likely due to variations in spawning success (Sonny et al. 2006). In this study, the catches compared to effort was higher in the pilot study in 2013 compared with the results from 2014 (41 larvae captured in 3-6 traps in 2013 compared to 107 captured in 24 traps in 2014, Figure 11;12). Further studies are needed to investigate variation in abundance of drifting larvae between years due to the large variation in discharge in this study area, influencing the catchability and the comparability of results between years.

Similar to the most common temporal pattern in fry drift, not only for grayling fry, but also other salmonids, cyprinids and percids (Gustafson-Marjanen & Dowse 1983; Bardonnet et al. 1993; Pavlov 1994; Reichard et al. 2002b; Oesmann 2003; Sonny et al. 2006), the grayling fry in Otta and Lågen mainly drifted during nighttime. Bardonnet et al. (1991) observed mainly nocturnal catches of drifting grayling fry in a small river in France. The diel pattern of the grayling drift was bimodal, with peaks at dusk and dawn (Bardonnet et al. 1991). In my study, the number of captures during the 12 h sampling interval only opened for separation between night- and daytime drift, but confirms the earlier observed nighttime drift of grayling fry also in large Nordic rivers.

The processes behind the observed nocturnal pattern in the drift of fish larvae have been linked to light intensity in several fish taxa, such as cyprinids, percids, Sockeye and Atlantic salmon (Gustafson-Marjanen & Dowse 1983; Fraser et al. 1994; Tabor et al. 1998; Reichard et al. 2002a; Oesmann 2003). The most common explanations used for nighttime drift relates to predation avoidance and loss of visual control (Pavlov 1994; Bardonnet 2001). The risk of accidental drift can increase in the dark because of loss of "visual landmarks" (Bardonnet 1993). The importance of daytime drift is often negatively correlated with water transparency and positively correlated with discharge, with the effect of discharge declining with improved transparency (Reichard et al. 2001; Oesmann 2003). Although this varies between rivers, it implies that the experienced light level by the larvae influences the propensity to drift. The observed nighttime drift pattern could also be influenced by differences in the catchability of the drift traps due to changes light intensity, with the grayling fry being able to control the drift into traps by day, but not at night. Scott (1985) reported that grayling fry started feeding before their yolk sacks were completely absorbed. The feeding pattern had peaks at dusk and dawn, which coincides with the earlier observed peak in grayling larvae drift (Bardonnet & Gaudin 1990b; Grimardias et al. 2012). One possible explanation of the diel variation in the drift can therefore be that the larvae get accidentally carried away by the current while feeding. However there is increasing evidence that the movement away from the emergence sites is a behavioral choice rather than an accidental displacement, with light-levels acting as cues rather than an explanation for the nightly drift patterns observed (Bardonnet et al. 1991; Bardonnet et al. 1993; Reichard et al. 2002a).

An adaptation to avoid predation could be another explanation for the nocturnal drift (Harvey 1991; Fraser et al. 1994). Although there is little information on predation of drifting fry, Carter and Reader (2000) assumed the fish larvae drift when low light levels reduces the risk of predation. Predation on sockeye salmon fry is observed to increase under periods of increased light levels (Ginetz & Larkin 1976). Increased light intensity is also observed to inhibit drift of Sockeye salmon fry, and the reduced migration is hypothesized to lead to higher rate of predation of passive fry (Tabor et al. 1998). Grayling is observed to emerge early in the morning, around sunrise (Bardonnet & Gaudin 1990a), but delay the drift until nighttime, using the substrate as a refuge against the current (Bardonnet & Gaudin 1990b).

Allan and Russek (1985) recommended use of several replicate samples rather than series of collections of 24 h samples for comparisons of drift densities between stream sections. In high intensity periods, sampling with several replicates was attempted to get more data. The large spatial scale of this study, the amount of stations and the distance between them meant sampling with several replicates was too time-consuming and thus unfeasible to handle for one man.

5.2 Spatial pattern

Most drifting grayling larvae were captured in the traps in the middle and at the bottom of the water column. This pattern is different from what has been observed for grayling fry drift before. Earlier studies of drifting grayling larvae have observed the larvae high in the water column, close to the surface (Bardonnet et al. 1991). This is common for cyprinidae and percidae who mainly drift close to the surface (Pavlov 1994; Oesmann 2003), but rare in other salmonids who mainly occupy the deeper end of the water column (Campbell & Scott 1984; Heggenes 1988). The high water transparency in Otta and Lågen might influence this pattern, as the earlier studied rivers might be more turbid (Oesmann 2003). The main factors influencing the position of drifting larvae in the water column are said to be hydro-physical (Pavlov et al. 2008), and the horizontal distribution patterns of drifting larvae are mainly determined by turbulence in the water flow (Pavlov et al. 2008). The pattern of grayling drift

deep in the water column was still common for all stations in this study, and shows a clear pattern in the vertical distribution. Control over vertical positioning in the drift has been observed for salmonids in previous studies, with Elliott (1987) reporting that trout fry appear to drift passively downstream at night and then return to the river substrate during daytime, indicating some manner of control on the vertical position during drift. The preference for deeper parts of the water column can be a mechanism for the larvae to control their drift, allowing them to settle in the river substrate when exiting the drift (Elliott 1987). The depth at which it was possible to handle the traps was limited, confining the stations in this study to shallow areas close to the river bank. The observed spatial pattern of drifting larvae might therefore not be representative for the deeper mid-river sections. Sampling in these sections are methodically challenging, so the drift trapping was confined to the areas close to the riverbank, where fry of both cyprinids and salmonids are known to drift (Brown & Armstrong 1985; Reichard et al. 2004).

The distances traveled by the grayling larvae emerging each night showed a rapid downstream displacement in both rivers (Figures 8&9). The estimations only accounted for passive nighttime drift, although the results indicate an active factor in the drift of larvae. This active factor is likely to influence each nights cumulated drift distances, with the fry drifting downstream slower than the current velocity indicates (Naesje et al. 1986). The estimated cumulated drift distances in this study shows the potential of drift as means of dispersal for fish fry. The results were very similar for both rivers, although they clearly differ in gradient and discharge. The little variation in measured water velocities between the rivers is likely linked to the positioning of the drift trapping stations were water velocities was measured. The drift trapping stations in the slow flowing parts of Lågen were positioned in areas with higher water velocities than the rather slow flowing section along Selsvollene, possibly overestimating the cumulated drift distances in Lågen. The use of drift traps is limited by a minimum current velocity for the traps to function properly, and a maximum flow velocity to avoid clogging of the traps. For the traps to function and have the possibility to catch larvae, the stations were placed in sections with a higher flow.

5.3 Environmental factors

The best model explaining the number of captured larvae included the environmental factors degree days (°D) and river. Temperature-dependent time of drift has been observed before, especially for larval cyprinids, who are known to drift after rapid increases in temperature (Sonny et al. 2006). Bardonnet and Gaudin (1991) showed how emergence of grayling was both temperature and light dependent in an artificial study system. Reichard et al. (2002b) showed how the drift of fish fry in two lowland European rivers was dependent on temperature rather than discharge, by influencing the timing of spawning. Jungwirth and Winkler (1984) argues that the use of day degrees are "at least questionable" when it comes to embryonic development of grayling because of the relationship between temperature and duration of development. The model of degree-days and its interaction with the rivers will therefore not necessarily be transferable to years with different water temperature patterns, although it is the model best explaining the drift of grayling larvae in 2014. Temperature is seldom found to have triggering effect on the drift of fish fry (Smith 1985; Naesje et al. 1986), but can have an effect on the drift through influencing the timing of spawning and development time from fertilization to emergence. The interaction between river and number of degree days until peak of drift observed in 2014 may illustrate an adaptation to the difference in temperature regime between the two rivers, as reported by Haugen (2000a)

While other studies have shown a relationship between daily discharge and number of drifting fish larvae (Ottaway & Forrest 1983; Naesje et al. 1986; Reichard & Jurajda 2004; Sonny et al. 2006), also for grayling (Grimardias et al. 2012), no such direct relationship was observed in this study. Further studies are needed to assess the influence of environmental factors on the drift of grayling larvae, but a purely descriptive assessment of the discharge patterns in relation to the timing of the drift 2013 and 2014 (Figure 11; 12) indicate that the timing of floods in relation to the emergence of grayling larvae can be important. Both as a cue for the larvae to start drifting, like it is observed for cisco and whitefish (Naesje et al. 1986), and for the spatial distribution of larvae. Harvey (1987) observed how the timing of floods can affect fish communities in different ways, dependent on both size and abundance of fish larvae at the time of the flood. A review of the drift literature shows there is a lot of factors possibly

influencing the drift, often in combination, illustrating the challenges with studying these drift systems (Heggenes 1988; Pavlov 1994; Zitek 2006).

5.4 Between-river differences

There was a difference in the longitudinal distribution of drifting grayling larvae between rivers. Grayling larvae were captured at all stations in Otta. In Lågen grayling larvae were only captured in the station Lågen1 directly downstream of the known spawning area and station 4, near the confluence and downstream of another spawning area. The lack of grayling captures in the more slow-flowing section along the stations Lågen 2 and Lågen 3 probably reflects the low number of drifting larvae drifting past these stations. In the low-gradient Lågen with little substrate heterogeneity and a laminar flow, grayling fry was observed maneuvering around the traps and settling along the river banks a couple of days into the drift period. It would be natural to interpret this as a sign that the first drift period was over, and that the larvae had settled in their first feeding habitat. With this amount of control there were no large drift dispersals, but presumably short, controlled downstream movements to new habitats. Compared with the high gradient and turbulent Otta where no grayling larvae was observed near the river banks, this illustrates the difference in drift patterns between the rivers, leading to a between-river difference in longitudinal distribution of young grayling. Øistad (2014) observed that the upstream parts of the high-gradient Otta was almost completely deserted by young grayling, and the abundance of young grayling increased in the lower reaches. This was not the case in the low-gradient Lågen where he found yearlings throughout the river, indicating less or shorter drift of grayling larvae. Øistad (2014) observed that the abundance of young grayling was associated with wide, slow-flowing river stretches in this study system. The high gradient in Otta, along with high valley confinement was the most important drivers of the distribution patterns observed in young grayling. This coincides with the observations made in this study off the longitudinal distribution patterns of drifting grayling larvae between the rivers and illustrates how the drift governs the spatial distribution of year of young grayling in the river system. In this study, the estimation of drift distances per night showed that most passive nighttime drifting grayling larvae in Otta would reach the nursing areas downstream of the confluence (Museth et al. 2011) within 2-3 nights. Similar estimates was made for grayling larvae drifting in Lågen, although observations of grayling

larvae along the banks of Lågen in the study area indicated they do not drift to the same nursing area as fry from Otta.

Grimardias et al. (2012) captured drifting grayling fry at two sites in a river in Switzerland. One directly downstream of a spawning site and another further downstream. Almost all the fry in the study was captured in the first site, leading to Grimardias et al. (2012) conclusion that the fry only drifted short distances, not reaching the second site before settling in a first feeding habitat, similar to the observations made of grayling larvae in Lågen. This differs from the observations made by Bardonnet et al. (1991), who observed a total desertion from a tributary with little nursery areas, similar conditions as observed in Otta, by drifting grayling fry. The difference between the two rivers in this study and the ones in the earlier studies illustrates the effect of varying river gradient, discharge patterns and distribution of first feeding habitat on the spatial drift pattern of grayling larvae.

In this study, three traps at each station, one in each height class, was assumed to be representative for the whole cross section of the river at each site. The different hydrological conditions among stations could have influenced the catchability at each site (Oesmann 2003). Differences in the general distribution patterns of drifting fish larvae can occur between locations in rivers due to turbulence and water velocity gradients across a river section, possibly redistributing the drifting larvae (Pavlov et al. 2008). This can explain some of the experienced variation in catchability between stations, as indicated by the station effect favored in the zero-inflation part of the ZIPme models (Table 4).

During the study period there was an increase in the total length of the captured grayling fry in Lågen, but not in Otta. The difference between rivers can be related to the different hydrological conditions, the main factor influencing the drift of fish fry according to Pavlov (1994). The higher gradient, discharge and water velocity is likely to influence the drift of fry (Naesje et al. 1986; Liebig et al. 1998; Grimardias et al. 2012), although no direct effect of discharge or water velocity was observed on the number of captured grayling larvae in this study. In higher water velocities with more turbulence the fry is more likely to get carried away by the current at emergence (Bardonnet & Gaudin 1990b). This can explain why there

was no increase in the length of captured grayling fry in Otta. All fry got carried away from the emergence site and drifted downstream. The section of Lågen within the study area is slow flowing, with a fine substrate riverbed. An explanation of the observed increase in length of drifting fry in Lågen can be that the water speeds were sufficiently slow for the fry to control its drift downstream by marginal displacements, like described by Grimardias et al. (2012), and use the area as first-feeding habitat. The rapid growth in days following emergence will leave the larvae able to control their movements in higher water velocities (Scott 1985; Deegan et al. 2005). During the first weeks after emergence the grayling fry has a rapid growth (Scott 1985; Bardonnet et al. 1991). Scott (1985) observed an increase in grayling fry length over three weeks following first emergence in a river used as first feeding habitat. This rapid growth is considered to be an adaptation for riverine fish fry, "allowing them to exploit periods of good resource availability in a stochastic environment" (Schiemer et al. 2002).

5.5 Drift as an adaptation in large migration systems

There are different theories about whether the drifting of grayling fry is passive or active. The typical water velocities in grayling spawning areas are much higher than the swimming capability of the grayling fry (Fabricius & Gustafson 1955; Scott 1985; Nykänen & Huusko 2002; Deegan et al. 2005), leading to the assumption that the fry is swept away with emergence (Grimardias et al. 2012). If the grayling larvae drifts passively, the peak in drift at night can be accidental and related to the loss of visual orientation (Pavlov 1994). If the grayling larvae simply drifted passively, an effect of discharge or measured water velocities at the different stations should be expected, but no such effect was observed. The clear pattern of nocturnal drift, concentrated deep in the water column and the lack of influence by discharge on the number of drifting larvae observed in this study is an indication that the larvae chooses to enter the drift, and can manipulate its position, rather than getting passively carried away with the current. Bardonnet and Gaudin (1990b) hypothesized the larvae could use the low water velocity close to the substrate to control their dispersal.

The behavioral nature of the drift observed in this study can be seen in light of the graylings ecology. The grayling seems well adapted to ensure drift dispersal of emerging larvae, being a spring spawner with emergence of larvae around the time of the floods, with high fecundity (Haugen 2000b), small eggs, shallow burial of eggs and small larvae at emergence (Northcote 1995). These early downstream migrations of young fishes are generally followed by upstream spawning migrations of adult fish (Pavlov 1994). Similar patterns are observed in some families of invertebrates who drift downstream as young and has compensatory upstream migrations as adults (Müller 1954; Müller 1974; Brittain & Eikeland 1988; Lancaster et al. 1996). A migration cycle allowing the drifting individuals to exploit the most favorable nursery areas downstream of the spawning sites, maximizing the species production potential in the river. Changes in discharge patterns and migration barriers influence the benefit of migration in regulated rivers and therein the underlying forces of long range within- of between- river migrations (Kraabøl & Nashoug 2010). The drift of grayling larvae might be an adaptation to large variations in flow between years and a driving force behind the migrations we observe of adult grayling, like its proposed for invertebrates (Brittain & Eikeland 1988), and a keystone in the goal to preserve migrating fish populations in large river systems.

The drift of larvae can also influence the area use of adult grayling in the study system. Adult grayling in Otta and Lågen was mainly observed swimming upstream after tagging in a radio telemetry study in both rivers (Museth et al. 2011). This can possibly be a life span migration, where the grayling compensate for drift as young by upstream migrations as adults and sub-adults. The drift of grayling fry from upstream spawning sites to common, slow flowing river sections in the lower reaches of Otta and to nursing habitat downstream of the confluence can be the reason behind the large home range sizes and complex migrations between both rivers in the study area (Museth et al. 2011) and why no genetic differentiation is observed in the grayling population in the study system, while differentiation is observed for the trout in the same system (Junge et al. 2014). Studies of genetic structuring of grayling populations in river systems illustrate how drift of fry ensures connectivity between tributaries and main stem populations, with more genetic variability in lower reaches of river systems (Meldgaard et al. 2003).

5.6 Management implications

The spatial and temporal distribution patterns of drifting fry in Otta and Lågen is interesting and highly relevant for fish management, as construction has started of a power plant at Rosten in Lågen, and the Norwegian Water Resources and Energy Directorate has recommended a re-development of the Eidefoss dam in Otta with a 10 km long minimum flow zone from Eidefoss through most of the study area in Otta. The grayling's use of large river systems through downstream migrations of larvae and upstream migrations for spawning illustrates the dynamic use of the rivers through the year. Whether and how hydropower developments may affect and change this dynamics is unknown. Diadromous and potamodromous fishes with extensive migrations between spatially separated seasonal habitats are generally sensitive to loss of connectivity due to regulation of rivers (Bunn & Arthington 2002). This can, to some degree, be mitigated by an adaptive management of flow. My observations of the spatial and temporal patterns of grayling larvae drift in Otta and Lågen can be useful for fish management in relation to new hydropower dams.

While earlier studies on the effect of hydropower dams on grayling migrations mainly have focused on the connectivity and spawning migrations of adult fish, little attention has been given to the effect of the regulation reservoir itself (Pringle 1997). The introduction of hydropower dams will likely affect the drifting grayling larvae by manipulating the water flow upstream of the dam, with the transition from flow-governed river habitat to slow reservoir flow. A transition from lotic to lentic habitat will likely end the drift of fry, not necessarily because of a physical barrier like the dam, but because of the change to reservoir flow (Copp et al. 1991). There is little knowledge about the use of reservoirs from riverine fish species, but studies of arctic grayling (*Thymallus arcticus*) indicate that reservoirs can act as barriers for grayling used to a lotic environment (Clarke et al. 2007). Increased predation from adult fish in reservoirs, and the possibility of introduction of predator species better adapted to reservoir flows, like pike (*Esox lucius*) and perch (*Perca fluviatilis*) can change the dynamics in the system (Kubečka 1993). The reduced fitness of drifting larvae, which no longer will drift to nursing areas, but to reservoirs, can change the selection from favoring migration towards favoring stationary behavior (Junge et al. 2014).

Downstream hydropower dams, a lower and more stable discharge will influence the drift of grayling fry. The life-history strategies in riverine fish species has developed in response to the natural flow regimes (Bunn & Arthington 2002). The fry depend on the water flow for dispersal to nursing areas. The development of grayling larvae is temperature dependent, and the number of degree days was the most important environmental factor influencing the drift of grayling in 2014. In rivers with reduced discharge as a consequence of hydropower regulation, the summer temperature often decreases while the winter temperature increases (Kvambekk et al. 2006; Tvede 2006). The change in temperature will likely influence the development period (Jungwirth & Winkler 1984) and thus the time of emergence and drift by grayling larvae. In Lågen, the construction of the Rosten dam is expected to have little effect on the temperature downstream, due to the run-off river regulation with a little reservoir (Museth et al. 2009).

The re-development of the Eidefoss hydropower plant in Otta will likely have a more pronounced effect on the drift of grayling larvae, both through changes in the temperature and discharge, especially in the proposed minimum flow section. The spawning sites below the Eidefoss dam is thought to be vital to preserve the long-range migration fraction of the grayling in the study area (Museth et al. 2011). The spatial patterns of the drift shown in this study indicates that the fry in Otta drift along the entire river section between the Eidefoss dam and the confluence, while drifting larvae in Lågen has access to nursery habitat between the spawning site and the confluence. This is supported by observations of young grayling made by Øistad (2014) and (Museth et al. 2011). The loss of connectivity between spawning sites and nursing areas through reduced drift in Otta will likely have a negative effect on the observed migration cycle of grayling in the Otta/Lågen river system. In Lågen, where the larvae use nursing habitats directly downstream of the largest spawning site at Grenet, no clear effects of regulation on the longitudinal distribution by drift of larvae is expected. The outlet from the dam at Rosten will be upstream of the known spawning grounds at Grenet, thus keeping the water flow from the spawning grounds to the nursery habitat, although a more stable flow with less daily variation must be expected (Museth et al. 2009). This will likely influence drift by changing the discharge patterns from natural fluctuation in the flow to artificial variations, possibly influencing cues for spawning, emergence and drift of grayling. Having river flow speeds at hand for the new maneuvering regime will make it possible to estimate drift-distance consequences under the new rules of operation.

Maneuvering regimes with release of water from the Eidefoss dam during the emergence period can aid the drift dispersal of grayling larvae from the spawning sites not laid dry in the minimum flow zone below the dam to nursery areas. The drift will often occur at the time of floods and the release of water to ensure drift of grayling should not be a problem most years. The problem will be if emergence and floods are not synchronized, like I observed in 2014. Then release of water is needed to maintain the drift of grayling larvae. The observed short drift period of grayling larvae indicate that release of water from the dam over a period of two weeks could be sufficient for the grayling larvae to drift to suitable habitat, although the reduced discharge in the minimum flow zone likely will prolong the drift period needed to reach suitable nursing habitat. A possible problem is to reliably predict the timing of the drift and thus the release of water. The results from the pilot study in 2013 and the main study in 2014 shows a very similar timing between the years, although time of spawning is thought to vary considerably (Museth et al. 2011). The main factor influencing the drift in 2014 was the number of degree days over 5°C. The number of degree days to peak drift was very similar in 2013 and 2014 in Otta, but there was large variation between the years in Lågen. Further monitoring of grayling drift over several years is needed to reliably predict the drift because of the uncertainties linked to the use of day degrees when it comes to early development of grayling (Jungwirth & Winkler 1984; Smith 1985), and between years variation in abundance of drifting larvae.

6 Conclusion

There are both spatial and temporal patterns in the drift of grayling fry in Otta and Lågen. The fry drifted over a short time period of 10-11 days, deep in the water column and mainly at night. While the grayling fry drifted over the whole study area in Otta, fry in Lågen only drifted short distances before settling in slow flowing nursing areas along Selsvollene. The number of degree days was the environmental factor best explaining the abundance of drifting grayling fry. The drift of grayling fry in Otta and Lågen is hypothesized to be a driving force behind the long range migrations and dynamic area use of both rivers observed in adult grayling in the study area. The development of hydropower regulation in these large

migration systems may affect the drift of grayling and be highly detrimental to the conservation of long range migration as life history strategy. Further knowledge on the environmental factors influencing drift of grayling larvae is needed for better management of these systems, included use of environmental flows and release of water to aid the drift of young fishes in regulated rivers.

7 Literature

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8 Appendix

Table A1: Drift traps used in Otta and Lågen from June 17 to July 7 2014, with trap ID, average water velocity (m/s) during the drift period, positions and days in use.

River	Trap ID	Average water velocity (m/s)	Coordinates (UTM)	In use (Day No.)	
				From	To
Lågen					
	1.1.A	0.389	32 V 523684 6856753	1	21
	1.1.B	0.347	32 V 523684 6856753	1	21
	1.1.C	0.255	32 V 523684 6856753	1	21
	1.2.A	0.396	32 V 523684 6856753	14	19
	1.2.B	0.374	32 V 523684 6856753	14	19
	1.2.C	0.278	32 V 523684 6856753	14	19
	1.3.A	0.277	32 V 523684 6856753	14	19
	1.3.B	0.233	32 V 523684 6856753	14	19
	1.3.C	0.164	32 V 523684 6856753	14	19
	2.0.A	0.355	32 V 526332 6855397	1	16
	2.0.B	0.350	32 V 526332 6855397	1	16
	2.0.C	0.278	32 V 526332 6855397	1	16
	3.0.A	0.291	32 V 528860 6852651	1	16
	3.0.B	0.279	32 V 528860 6852651	1	16
	3.0.C	0.187	32 V 528860 6852651	1	16
	4.0.A	0.725	32 V 528737 6848796	1	21
	4.0.B	0.675	32 V 528737 6848796	1	21
	4.0.C	0.452	32 V 528737 6848796	1	21
Otta					
	1.1.A	0.540	32 V 516306 6852303	1	21
	1.1.B	0.451	32 V 516306 6852303	1	21
	1.1.C	0.349	32 V 516306 6852303	1	21
	1.2.A	0.413	32 V 516306 6852303	10	18
	1.2.B	0.326	32 V 516306 6852303	10	18

1.2.C	0.242	32 V 516306 6852303	10	18
1.3.A	0.458	32 V 516306 6852303	10	18
1.3.B	0.360	32 V 516306 6852303	10	18
1.3.C	0.359	32 V 516306 6852303	10	18
2.1.A	0.431	32 V 518720 6851743	1	21
2.1.B	0.383	32 V 518720 6851743	1	21
2.1.C	0.330	32 V 518720 6851743	1	21
2.2.A	0.407	32 V 518720 6851743	16	20
2.2.B	0.400	32 V 518720 6851743	16	20
2.2.C	0.351	32 V 518720 6851743	16	20
2.3.A	0.352	32 V 518720 6851743	16	20
2.3.B	0.342	32 V 518720 6851743	16	20
2.3.C	0.261	32 V 518720 6851743	16	20
2.4.A	0.314	32 V 518720 6851743	16	20
2.4.B	0.314	32 V 518720 6851743	16	20
2.4.C	0.224	32 V 518720 6851743	16	20
2.5.A	0.249	32 V 518720 6851743	16	20
2.5.B	0.256	32 V 518720 6851743	16	20
2.5.C	0.181	32 V 518720 6851743	16	20
3.0.A	0.382	32 V 520930 6850304	1	16
3.0.B	0.318	32 V 520930 6850304	1	16
3.0.C	0.274	32 V 520930 6850304	1	16
4.0.A	0.530	32 V 528769 6848280	1	21
4.0.B	0.512	32 V 528769 6848280	1	21
4.0.C	0.348	32 V 528769 6848280	1	21

8.1   Model selection tables

Table A2: Complete AIC model selection table for the Zero- models in the ZIP models of grayling fry drift in Otta and Lågen in 2014. For the selection process the count- model was fixed with the variables River * Day^2. ΔAIC= deviation relative to the most supported model.

Zero-modell	AIC	ΔAIC
River site + Height	329.4	0
River site	339.9	10.5
Height	341.2	11.8
Ln distance to spawning area	344.8	15.4
River	344.9	15.5
Standardized discharge	345.1	15.7
Water temperature	345.5	16.1
Distance to spawning area	345.5	16.1
Water velocity	345.5	16.1
Water velocity^2	346.2	16.8
River site * Water velocity^2	347.1	17.7

Distance to spawning area^2	347.2	17.8
River station * Height	349.3	20.0
River site * Water velocity	351.5	22.1
Trap ID	358.4	29.1

Table A3: Complete AIC model selection table for the count-models from the ZIP models of grayling fry drift in Otta and Lågen rivers in 2014. For the selection process, the most supported zero-model was used (River site + Height). ΔAIC= deviation relative to the most supported model.

Count-modell	AIC	ΔAIC
Degree days^2 * River	324.9	0
River + day^2	329.2	4.3
River * day^2	329.4	4.5
Standardized discharge + day^2	329.8	4.9
day^2	330.8	5.9
Water velocity^2 + day^2	331.3	6.4
Water velocity + day^2	332.3	7.4
Distance to spawning area + day^2	332.7	7.8
Water velocity * day^2	333.8	8.9
Degree days^2 *Standardized discharge	333.9	9.0
Degree days^2 + Standardized discharge	339.6	14.7
River site + day^2	341.0	16.01
Degree days^2 + River	344.3	19.4
Degree days^2 + Distance to spawning area	344.8	19.9
Degree days^2 + Water velocity^2	345.0	20.1
Degree days^2 * Water velocity	347.0	22.1
Water velocity	355.6	30.7
River	355.9	31.0
Day	356.2	31.3
Degree days	356.3	31.4
River * Standardized discharge	356.4	31.5
Distance to spawning area	356.5	31.6
River + Standardized discharge	356.7	31.9
River + Water velocity	356.8	31.9
Water velocity^2	356.9	32.0
River + Day	357.9	33.0
River + Distance to spawning area	358.0	33.1
River * Degree days	358.5	33.6
River + Water velocity^2	358.5	33.6
Height	358.7	33.8
River * Day	358.8	33.9
River * Distance to spawning area	360.0	35.1
River * Water velocity^2	362.5	37.6

River site	363.7	38.8
River site * Height	364.0	39.1
River site + Height	368.5	43.7