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Migration, growth patterns, and diet of pike (*Esox lucius*) in a river reservoir and its inflowing river

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Abstract

The pike population in the Løpsjøen reservoir and the accessible 21 km section of the inflowing River Rena was investigated from 2003 to 2013. Telemetry and mark-recapture with Floy tags demonstrated that most fish had an annual home range of less than 2 km, while some fish performed quite extensive migrations (up to 14.4 km). Of fish radio-tagged in the reservoir, 57% were positioned in the river at least once. The population of pike ≥ 25 cm was estimated at 1002 fish, or 3.9 fish (3.17 kg) ha^{-1}. Mean length at age was significantly larger for pike caught in the river than in the reservoir for almost all age groups. CPUE during boat electro-fishing indicated significantly lower population densities and a lower proportion of juvenile fish in the river than in the reservoir. Diet analysis revealed that almost all available prey fish species were taken by pike, and that there was a clear diet differentiation between pike size classes, and between fish from the river and reservoir habitats. Small pike (<25 cm) in the reservoir had eaten mainly invertebrates, whereas smaller pike and Alpine bullhead (*Cottus poecilopus*) dominated in small pike from the river. Nine prey fish species were identified in the stomachs of medium sized pike (25-50 cm) in the reservoir, with brook lamprey (*Lampetra planeri*) and brown trout (*Salmo trutta*) as dominant. Medium sized pike in the river had taken mainly lamprey and Alpine bullhead. Larger pike (>50 cm) in the reservoir had taken brown trout as well as a number of other prey fish, while river pike of this size had taken burbot (*Lota lota*), lamprey and brown trout. Species like perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and in particular grayling (*Thymallus thymallus*) were rarely found in pike stomachs. The construction of the reservoir in a fast-flowing river caused the establishment of a healthy pike population and additional predation pressure on the rheophilic salmonids in the system, both in the reservoir and in the inflowing river.

Keywords

River fragmentation, predation, habitat utilization, habitat modification, northern pike

1 Introduction

Fragmentation of river habitats is recognized as a major threat to the natural function of rivers, and specifically to the life cycle of migratory fish species (Jungwirth, 1998; Zitek et al., 2008; Liermann et al., 2012). Dams causing reduced connectivity are a challenge in all types of rivers. In fastflowing rivers, with a fish community dominated by rheophilic species like the salmonid brown trout (*Salmo trutta*) and European grayling (*Thymallus thymallus*), the lake habitat created in the reservoir above the dam constitutes an additional negative impact on the native fish community. The transformation of the habitat from one dominated by fast water currents to a lentic habitat reduces the total area of suitable lotic habitat, and it brings about a transformation of the fish community from a dominance by rheophilic to limnophilic species. Depending on the species present upstream in the watershed, the reservoir fish community would be expected to include predators like, e.g., northern pike (*Esox lucius*) and Eurasian perch (*Perca fluviatilis*) (cf. e.g. Jepsen et al., 2000). In fast-flowing rivers, these predators would normally only be found in low numbers in shallow backwaters. Reproducing populations may be associated with lakes, and the establishment of a new reservoir will provide a colonization opportunity (cf. Sandlund et al., 2007). Besides the frequently mentioned negative impacts of dam construction like barrier to migration and loss of habitat, the increased predation pressure from limnophilic predators established in reservoir is rarely studied (cf. Lasne et al., 2007).

Northern pike is a limnophilic species associated with lakes and slow-flowing rivers, and it is the common top predator in northern inland waters. In many countries it has a commercial and recreational value (Raat, 1988), but in rivers with a good recreational fishery for salmonids like brown trout and European grayling, the establishment of any new pike population is considered a negative consequence of any impoundment or reservoir.

Northern pike is commonly associated with macrophyte vegetation in shallow waters (Chapman & Mackay, 1984; Bry, 1996), but in particular larger individuals also often utilize open waters (Vehanen et al., 2006). Many studies have reported on the habitat use and trophic ecology of pike in lakes and

slow flowing rivers (Mann, 1982; Vøllestad et al., 1986; Koed et al., 2006; Ovidio & Philippart, 2003; Winfield et al., 2012). However, little has been reported on how northern pike established in a river reservoir would utilize the upstream fast-flowing river habitat. Would pike exert a predation pressure even in the river, or would the rheophilic salmonids find a refuge from pike predation by remaining in the river habitat?

To throw light on this issue, we have investigated habitat use and diet of pike in a river reservoir and the associated upstream river habitat. Our main hypothesis would be that pike mainly utilize the limnetic habitat in the reservoir, and rarely venture into the fast-flowing river. Thus, predation pressure from pike would likely be restricted to those rheophilic individuals that move into the reservoir.

Our results are discussed with a view to better understand the impact this predator may have on the rheophilic fish species in such a modified river section.

2 Material and methods

2.1 Study area

Our study area is a section of the River Søndre Rena (hereafter River Rena), which is a major tributary to Norway's largest river, Glomma (WCD, 2001; Østdahl et al., 2002). The study section of River Rena (Fig. 1) is 25 km between the Storsjø dam at the outlet of Lake Storsjøen (250 m a.s.l.), and the Løpsjø dam, which creates the reservoir Løpsjøen (altitude: 235.5 m a.s.l., length: 4 km, surface area 1.73 km^2, maximum depth 15 m, maximum drawdown 1 m; more details in Museth et al. (2006), Sandlund et al. (2007)). Lake Storsjøen is a natural, large and deep fjord lake (47.5 km^2, max. depth 309 m), with a moderately regulated water level (amplitude 3.7 m), and a fish community containing the same species as the Løpsjøen reservoir (details in Museth et al. (2008)). The Storsjø dam was constructed in 1969, the Løpsjø dam in 1971. Fishways were constructed in both dams, but the functionality of the fishways is limited, and only the rheophilic species (mainly brown trout, *Salmo trutta*, and European grayling, *Thymallus thymallus*) are to some extent able to pass them in an upstream direction (Museth & Qvenild, 2003). Downstream passage is probably possible through floodgates and turbines (at the Løpsjøen dam), but this has not been studied.

89 The Løpsjøen reservoir is situated where there previously was a section of swiftly running river. The
90 elongated Løpsjøen basin is between 200 and 600 m wide. The forest on the inundated land was
91 removed before damming. Excepting the dam itself, the present riparian areas are covered by boreal
92 forest, mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). While the littoral zone in
93 the lower approx. 2.5 km of the reservoir are steep and with little macrophyte vegetation, a
94 relatively species rich aquatic macrophyte vegetation is found along the shores and in shallow bays in
95 the upper 1.5 km (Museth et al., 2006). The mean annual flow in River Rena is 108 m^3 sec^{-1}, and the
96 mean gradient over the 21 km of the remaining lotic habitat from the Storsjø dam to the upstream
97 end of the Løpsjøen reservoir (cf. Fig. 1) is 0.7 m km^{-1}. Thus, the river fragment between the barriers
98 consists of 4 km lake-like reservoir and 21 km of river. The river channel is relatively deep (3-4 m),
99 narrow and confined, but there are occasional narrow patches and small backwaters of shallow
100 vegetated areas along the shore. The riparian areas are completely dominated by boreal forest, only
101 a total of approx. 2 km along the 2 x 21 km of riverbank is cultivated land. There are only a few points
102 with physical constructions, e.g. bridges.

103 Due to the high mean water flow in the Rena River and the restricted volume in Løpsjøen reservoir,
104 the theoretical retention time is short (approx. 0,85 days), and water quality in the river and
105 reservoir is more or less identical. Water quality monitoring in the Rena River in 2000-2005 at
106 sampling stations just above and below Løpsjøen, showed pH = 7.0-7.3, total organic carbon (TOC,
107 mg C l^{-1}) 2.6-4.9, and turbidity (FNU) 0.3-0.9 (Løvik & Rognerud, 2006).

108 Ten fish species were recorded in the Løpsjøen reservoir: brown trout, European grayling, whitefish
109 (*Coregonus lavaretus*), northern pike, European perch, roach (*Rutilus rutilus*), European minnow
110 (*Phoxinus phoxinus*), Alpine bullhead (*Cottus poecilopus*), burbot (*Lota lota*), and brook lamprey
111 (*Lampetra planeri*) (Museth et al., 2006; Sandlund et al., 2007). Catches during extensive survey net
112 fishing in the reservoir in June and August 2003 (total catch 438 fish) resulted in 45 % perch, 22 %
113 whitefish and 20 % roach. The rheophilic species brown trout and European grayling constituted only
114 1 % and 2 %, respectively (Museth et al., 2006). Routine survey net fishing rarely catch northern pike,
115 and boat electro-fishing have shown a dominance of pike and perch in the reservoir (see Results).
116 Additional fishing to catch pike has indicated that pike rarely move at greater depths than approx. 2
117 m.

118 During the early years of the study period, 10,000 brown trout with a mean length of 20 cm were
119 stocked annually in River Rena between the Løpsjøen reservoir and the Storsjø dam to compensate
120 for the assumed production loss due to hydropower development. Due to the removed adipose fin

121 on all stocked fish, it was possible to identify 50% of the brown trout in gillnet catches in 2003 as
122 stocked fish.

123 2.2 Material

124 Data was collected on pike in the Løpsjøen / River Rena study area during various projects between
125 2003 and 2013, and has included telemetry for studies of migration, mark-recapture for migration
126 and population estimates, and collection of fish to analyse habitat use, population parameters and
127 diet. Fish for ageing and diet analysis were sampled over the months May-September during 2003-
128 2004, 2007-2009 and 2011 (Table 1). The majority of pike for ageing and diet analysis were caught in
129 June and July, as catchability, both by nets and by angling, is higher in early and mid summer. The
130 catch effort was restricted, in order not to unduly influence pike population numbers in the relatively
131 restricted habitat area of the river and reservoir. Consequently, the fish samples had to be pooled, as
132 appropriate, within years, within size groups, and within habitats.

133 In spite of data collection for various purposes over a series of years, we consider the environmental
134 conditions of the study area to be quite stable from year to year. Boat electrofishing in the river
135 habitats in the years 2008 – 2012 showed that the salmonids brown trout and grayling constituted 61
136 – 76% of the annual catches, i.e. they were the dominating fish species. Alpine bullhead was the third
137 dominating species and constituted 6.9 – 16 % of the annual catches (Museth et al., 2013). Apart
138 from the hydropower regulation, which results in a relatively stable water flow in River Rena from
139 year to year, there is little human impact on water quality (Taugbøl et al., 2004; Museth et al., 2006).

140 The age of pike was determined by reading the metapterygoid bone (Sharma and Borgstrøm, 2007)
141 in 123 fish from River Rena and 157 fish from Løpsjøen reservoir (Table 1). To reduce handling stress,
142 pike for tagging was not weighed. Thus, in biomass estimates, the following length – weight
143 relationship was applied, based on the length (cm) and weight (g) of 92 pike between 23.5 and 112
144 cm mainly caught in the reservoir in June and August 2003, and June, July and September 2007: $L = 0.063 \ln W + 3.414$, $R^2 = 0.93$.

146 During May 12-19, 2003, 135 pike between 25 and 79 cm in length were caught by various methods
147 (nets, traps, angling) at spawning sites (Fig. 1) and tagged with Floy tags. The fish had running
148 gonadal products. Subsequent catches of pike were performed through 2003 (June 5 – September
149 29) and 2004 (April 30 – July 9). For fish captured during this period, back-calculation based on the
150 metapterygoid bone was applied in order to verify which individuals were within the length of 25-79
151 cm at the time of Floy-tagging. A total of 241 fish were caught belonging to this group, including 35

recaptures of Floy-tagged fish. These results were the basis for a Petersen estimate of population numbers (Ricker, 1975).

Between June 17 and July 4, 2003, 19 pike (body lengths 51.5-73 cm, Table 2 and Fig. 1) were caught in the area of the upper end of Løpsjøen reservoir and lower part of River Rena, and tagged with internal radio transmitters (Advanced Telemetry Systems (ATS), model F1835, weighing 13 g, and F1840, weighing 20 g). The position of the pike was determined during one year from June 2003 to June 2004 using an ATS Challenger Receiver R2000 and a folding Yagi antennae. In the summer season, tracking was done from boat, twice weekly over the 5 km of river immediately upstream of the Løpsjøen reservoir, (cf. point 2 in figure 1) and the reservoir itself, and once per month for the whole study area. In the winter season, from November 2003 until March 2004, tracking was done monthly from fixed positions on land over the whole study area (from the Storsjø dam to the Løpsjø dam). The total number of detections of pike during the study period was 863 (Table 2). Locations were recorded as distance (km) upstream the Løpsjøen dam to the nearest 0.5 km zone. Home ranges were calculated for each radio-tagged fish, and were equal to the length of the river/reservoir section which included all positions. A detailed description is available in Taugbøl et al. (2004).

A total of 405 pike were dissected for analysis of stomach content (Table 1). In River Rena, 123 pike between 13 and 98 cm in length, caught from 2007 to 2011, were analyzed. Of these stomachs, 41.6% contained no prey. In Løpsjøen reservoir, 282 pike between 8 and 112 cm in length, caught from 2003 to 2007, were analyzed. Of these stomachs, 36.2% contained no prey. Although samples for stomach analysis to some extent were collected during different years in the river and the reservoir, there was no indication that stomach contents changed from year to year. The fact that the samples were collected over the same months appear to justify a comparison between river and reservoir. The stomach contents were analyzed with a focus on prey species, and the results are shown as the prevalence of each prey type in the analyzed stomachs and the percent wet weight constituted by the prey type over all stomachs. In order to be able to compare diet between the river and reservoir habitats in three size groups of pike, the results of diet analysis were pooled for all months of sampling (May-September).

As part of the monitoring programme for this river fragment both River Rena and the Løpsjøen reservoir were sampled annually from 2008 to 2013 by an electrofishing boat (Smith-Root model EH 18 with a 7.5 kW pulsator) (Table 1). Fishing was done along the same defined transects each year (mean, maximum and minimum length of each transect: 564, 1100, 192 m). Catch per unit effort is reported as number of fish caught per minute of fishing (number of seconds with electric voltage in the water registered by the pulsator), which is the common unit in boat electrofishing studies (e.g.

Bajer & Sorensen, 2012). All fish caught during these surveys were identified to species and their body length was measured before being released back into the water.

3 Results

Comparison of length-at-age of pike caught in the Rena River and in the Løpsjøen reservoir demonstrated that fish from the river were significantly larger at age than fish from the reservoir for all age groups except age-2 (Fig. 2).

Population estimates based on mark-recapture with Floy tags (Petersen estimates) in 2003-2004 resulted in an estimated number of 672 fish in length group 25-49.9 cm (95% c.l. 397-1213), and 330 fish ≥50 cm (95% c.l. 224-508). Thus, at that time, the total number of pike larger than 25 cm in the study area was a little over 1000 fish. This corresponds to a density of 3.9 fish ha^{-1}, or 3.17 kg ha^{-1}.

The movement of radio-tagged northern pike recorded for one year after tagging demonstrated that most fish remained relatively stationary, with 10 out of 19 fish with a home range of less than 2 km (Fig. 3A). A few fish moved further afield, with two fishes covering 5.3 and 14.4 km, respectively. (For details, see Appendix 1). The pattern of migration distances in pike was also confirmed by the recaptures of Floy-tagged pike (Fig. 3B). A total of 15 pike tagged during the spawning period in 2003 were recaptured during the spawning one year later (Fig. 3B). Of these, 80% (n=12) were recaptured < 100 m from the tagging site, while the remaining three were recaptured 190, 800 and 1280 m from the tagging site. Observed recaptures outside the spawning season (n = 20) were more dispersed, although most of them were also recaptured quite close to the tagging site. Of these recaptures, 30% were recaptured less than 100 m from the tagging site, while 80% were recaptured less than 1000 m from the tagging site. The remaining four fish were recaptured 1700, 2300, 5400 and 10 800 m, respectively, from the tagging site (Fig. 3B).

Among the radio tagged pike (N = 19), eight (42 %) were positioned in both River Rena and the Løpsjøen reservoir during the tracking period of one year. Of eight pike radiotagged in the reservoir, five (62 %) were subsequently positioned at least once in the river, but only 2.1 – 12.8 % of their positions during the year were in the river. Of 11 pike radiotagged in the river, three (27 %) were subsequently positioned at least once in the reservoir.

This shows that a large proportion of the fish move between the habitats, despite having relatively restricted annual home-ranges.

The length distribution and catch per unit of effort (no. of fish per minute of fishing with the electro fishing boat) indicated that the density of pike was lower in the river than in the reservoir (Fig. 4).

The median value of catch per minute boat electrofishing varied within the reservoir (0.07 – 1.34) and the river sections (0 – 0.16), but the median values of CPUE were significantly higher in the reservoir (0.21) than in the river (0.02) (Mann-Whitney Rank Sum Test, $P < 0.001$). The proportion of pike ≤ 20 cm, corresponding to 0+ and 1+ pike, was significantly higher in the reservoir than in the river ($\chi^2 = 6{,}201$; $P = 0.013$).

The stomach contents of small pike (<25 cm in length) in the reservoir were completely dominated by invertebrates, both in terms of frequency of occurrence and percent wet weight (Fig. 5). The invertebrates taken were mainly aquatic insects, i.e., Trichoptera larvae and Odonata nymphs (chiefly dragonflies), but occasionally also the crustacean *Gammarus lacustris.* A very limited amount of small whitefish and minnow was also taken. In contrast to this, small pike in River Rena had mainly eaten fish, with smaller pike and Alpine bullhead as the main prey species. Various invertebrates, mainly insects, commonly occurred in small pike in the river, but in a low proportion of the stomach content wet weight. Burbot, lamprey and brown trout were also found in the stomachs of small pike from the river.

Medium-sized pike (25-49.9 cm) caught in the reservoir had taken more prey fish than smaller pike in this habitat, and a total of nine fish species were identified in the stomach content (Fig. 5). Pike, lamprey and brown trout were the most prominent, but six other fish species combined to constitute a prominent contribution (Fig. 5). This included perch, whitefish, burbot, minnow, roach and Alpine bullhead. In the river, fish was an important prey for this size group of pike, but only lamprey, Alpine bullhead, pike and brown trout were identified as prey fish. Invertebrates were commonly found in the pike stomachs, but constituted a moderate proportion of the stomach content wet weight. Stomachs of medium-sized pike contained the same groups of invertebrates as found in small pike.

Brown trout was a prominent prey in large pike (≥50 cm) in the reservoir, but a number of other fish prey were also taken (Fig. 5). This included pike, whitefish, lamprey, burbot, Alpine bullhead, minnow and perch. In River Rena, the stomach content of large pike was dominated by burbot, brown trout and lamprey. Pike, Alpine bullhead, whitefish and minnow were also identified, and this was the only case where grayling was identified in the stomach content of pike. Two individual pike (out of 81 fish) had remains of grayling, which constituted less than 2% of the stomach content wet weight in this group of pike.

Boat electrofishing showed large differences in the composition of the fish community in the river and reservoir, indicating different availability of prey species for pike. Brown trout and grayling constituted 70% of the catches in the river habitat, whereas these species constituted 15% of the catches in the reservoir (Fig. 5). In the reservoir, pike and perch were the dominant species and

constituted 67% of the catches, whereas these species constituted no more than 3% of the river catches.

Brown trout occurred in pike stomachs on all sampling occasions. It should, however, be noted that in pike sampled within two weeks after release of the stipulated hatchery-reared brown trout (mean size 20 cm) in River Rena, brown trout constituted an unusual proportion of pike stomach content in the Løpsjøen reservoir. This occurred in both 2003 and 2004. On these occasions, 65% of large pike had brown trout in their stomachs, and 83% (24 of 29 fish) of the prey fishes could be identified as hatchery-reared, based on the removed adipose fin in all released fish. Pike sampled more than two weeks after the stocking event in these two years had to a much lesser extent eaten brown trout. We do not, unfortunately have pike samples from the river in 2003 and 2004 (Table 1), so the possible predation on hatchery brown trout in the river cannot be analyzed.

There was a significant correlation between predator length (L_{pike}) and prey length (L_{prey}) in the combined data from River Rena and the Løpsjøen reservoir (Fig. 6). However, it should be noted that even large pike may eat relatively small prey fish. For example, pike around 200 mm had eaten prey from approx. 15 mm (a burbot) to 120 mm (a pike), while pike around 600 mm in length had eaten prey from approx. 30 mm (a minnow) to 250 mm (a brown trout).

4 Discussion

Pike in the Rena River and the Løpsjøen reservoir utilized both the reservoir and the river. Radiotracking indicated that most pike had a restricted home range of less than 2-3 km within an available river-reservoir section of 25 km, although some of these fish also moved between river and reservoir. A majority of pike tagged in the reservoir was later positioned at least once in the river. A few fish, however, moved over longer distances, up to 12-14 km, thereby utilizing approx. 50% of the available river fragment. Our recaptures of Floy tagged fish indicated a similar distribution of migration distances among the pike.

The apparent return to the same spawning grounds one year after tagging seem to indicate repeated homing in these multiple spawners (cf. Frost and Kipling, 1967; Bry, 1996). Whether this reflects homing to the spawning site where the fish was hatched is not known, although natal homing has been shown in some pike populations (Engstedt et al., 2014). Site fidelity of repeat spawners may offer an opportunity for management to more effectively reduce the population of this unwanted predator. For a part of the year, fish were tracked once per month, and some short-term movement may therefore have been missed (Baktoft et al., 2012, Pauwels et al., 2014). However, a similar pattern of individual variation in movement, showing both stationary and extensively moving fish,

has also been recorded in other studies of pike (e.g. Jepsen et al., 2001; Vehanen et al., 2006; Kobler et al., 2009).

Surveys by electrofishing boat along River Rena and the Løpsjøen reservoir in late summer indicated a higher density of all size groups of pike in the reservoir. The size distribution indicated also that the occurrence of small or juvenile pike in the river was relatively restricted. This may indicate that recruitment to the pike population within this river/reservoir fragment mainly occurs in the reservoir, and that the river section to a large extent is colonized by older pike seeking feeding opportunities. Our direct observations also indicate that the main spawning of pike occurs in the reservoir. However, the extent of cannibalism in pike <25 cm in the river may indicate that some spawning occurs there. The fact that pike in the river were significantly larger than pike in the reservoir in almost all age classes may indicate that the individuals with the highest growth rate moved from the reservoir to the river, but this may also be a density-dependent effect (Haugen et al., 2007). Our data from boat electrofishing indicated that pike density was much lower in the river. Thus, there might be more available prey fish for pike in that habitat. The prominence of fish prey in the stomachs of small pike in the river may reflect more accessible small fish prey, which may cater for better growth. One rheophilic prey species, which was prominent in the stomachs of small pike, was Alpine bullhead. Boat electro fishing indicates that this species was not as common in the reservoir as in the river.

In general, the growth of pike in the Rena River and the Løpsjøen reservoir is moderate, fitting well with the "growth standard" published by Casselman (1996). Vøllestad et al. (1986) investigated pike growth in other Norwegian lakes and found that 10 year old pike typically was 75-80 cm in length. Compared to this, mean length of pike 10 years and older caught in the Løpsjøen reservoir was smaller (69.5 cm) while pike caught in the Rena River was larger (94.3 cm). The difference in length at age between fish from the lotic and lentic habitats, with riverine fish growing faster, seems to be in opposition to the results reported by Penczak (2007). He found that lake pike grew better than river pike. However, in a meta-analysis of pike growth across North America and Eurasia, Rypel (2012) found no systematic difference in pike growth between habitat types.

We estimated the total biomass of pike >25 cm in the river and reservoir at 3.17 kg wet weight ha^{-1}. We do not have data on production and seasonal consumption by pike, but rough estimates based on the daily rations published by Diana (1979), may indicate a daily consumption of fish prey at approx. 7-11 kg wet weight ha^{-1} day^{-1}. This indicates that pike predation may be a significant mortality factor for prey fish populations in both the reservoir and the river.

The range of prey species observed in the stomachs of pike in the river-reservoir system supports the notion of pike as an opportunistic predator. Of the fish species prominent in the study area, only perch, roach and grayling occur very rarely in the stomach content of pike. Some reports indicate that pike select against perch as prey when other prey species are readily available, possibly due to the spiny fins of perch (Beyerle and Williams, 1968; Mauck and Coble, 1971). However, it seems that habitat characteristics, which provide shelter for prey fish and thus may reduce the hunting efficiency of pike, may be more important for prey selection (Eklöv and Hamrin, 1989). In our study area, macrophyte vegetation constitutes the main shelter, and the extent of vegetation is larger in the reservoir than in the river.

In lakes, roach is a common prey for pike, but the roach population in the Rena River and Løpsjøen reservoir is restricted and constituted only 1.2% and 0.78%, respectively, of the total boat electrofishing catch. Considering the abundant grayling population in the Rena River, it is quite surprising that this species seems very rarely to be taken by pike. It may be speculated that the habitat choice by grayling is the reason for this. Grayling tend to live in the water masses away from the substratum and, at least in the river, out in the relatively fast currents (e.g., Mallet et al. 2000). This may be habitat conditions where the hunting technique of pike is less efficient.

The prominence of lamprey in the stomachs of pike from the Rena River and Løpsjøen reservoir was somewhat surprising, although lamprey as a prey for pike has been documented before (e.g., Sepulveda et al., 2013). The only group of pike without this species in the stomachs was small pike from the reservoir. Still, only a few individuals of lamprey were caught by electroboat fishing, indicating either that the species is positively selected by pike or that it is substantially underrepresented in electroboat catches.

The opportunistic feeding habits of pike are further indicated by the dominance of brown trout in the stomachs of large pike captured within two weeks after the release of naïve prey in the form of hatchery-reared brown trout. This is in line with other reports on the relationship between stocked hatchery produced salmonids and pike (Lepak et al., 2014), and indicates that strategies for brown trout stocking in waters with pike need to consider this additional and sometimes dramatic mortality factor.

Our results indicate that the construction of Løpsjø dam and the associated formation of the Løpsjøen reservoir have created a suitable habitat to facilitate the establishment of a substantially increased pike population. There might have been a sparse population of pike in the river before the establishment of the Løpsjøen reservoir, although unpublished information from the hydropower company (T. Taugbøl, GLB, pers. comm.) indicate that the habitat conditions would have allowed no

pike to live in the rapids where the dam and the lower part of the reservoir now stand. Pike from the river as well as from Lake Storsjøen would have been able to quickly move downstream and colonize the reservoir. We do not have data to indicate how fast this happened, but survey fishing in 1981 (ten years after the dam construction) identified a healthy pike population in the reservoir (Taugbøl et al., 2004). Other lake fish species have also established populations in the reservoir, such as perch, roach and whitefish (Sandlund et al., 2007). While the remaining lotic section of the Rena River upstream from the Løpsjøen reservoir apparently does not provide the best habitats for pike recruitment, subadult and adult pike are able to live along the margins of the river and constitute a substantial predation pressure on several riverine fish species. Of most concern to management is the predation on brown trout, while grayling, somewhat unexpectedly, to a large extent seems to avoid predation. The observations of pike predation on stocked hatchery reared brown trout in the Rena River and Løpsjøen reservoir is the main reason for the termination of the stocking program in 2013 (Museth et al., 2013).

In conclusion, our hypothesis that pike did not venture into the fast-flowing river must be rejected. Although densities of pike are lower in the river than in the reservoir, pike still exerts a substantial predation pressure on rheophilic species in the river. The relatively good growth rates of pike in the river may also indicate abundant food resources in this habitat. For the combined river/reservoir section, the establishment of the Løpsjøen reservoir has quite clearly increased predation pressure on brown trout, which is the most attractive target species for anglers and, together with European grayling, the basis for fishing license sales in this river.

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Table 1. Number of pike sampled and analyzed for age and stomach contents each year in River Rena and Løpsjøen reservoir (cf. figure 1), 2003 – 2013, and the number of pike caught by boat electro fishing 2008-2013.

Activity	Stomach analysis		Ageing		Boat electrofishing	
Year	Reservoir	River	Reservoir	River	Reservoir	River
2003	139		106			
2004	51		51			
2007	92	6		6		
2008		37		37		5
2009		11		11		12
2010						20
2011		69		69		23
2012					30	9
2013					78	

Table 2. Summary of the biometric, tagging and movement data of 19 northern pike radiotagged in River Rena and the Løpsjøen reservoir in 2003. See also Appendix 1. All fish, except no. 433, were tracked for approx. one year.

Fish no.	Date	Tagging habitat	Length (cm)	Weight (g)	Tag weight (% of fish weight)	No. of detections	Max. distance from tagging site (m)	Max distance between two positions (m)
403	17.06.	Reservoir	54	803	1.62	48	2053	2751
412	18.06.	River	55	819	1.59	52	421	654
423	18.06.	River	72.5	1097	1.82	54	423	610
433	19.06.	Reservoir	54	803	1.62	7	721	721
442	19.06.	Reservoir	62	930	1.40	46	2214	2712
454	19.06.	Reservoir	51.5	763	1.70	45	2488	2492
466	19.06.	Reservoir	63.5	954	1.36	48	3140	1309
475	19.06.	River	59.5	890	1.46	53	4490	5233
485	19.06.	River	52	771	1.69	51	822	822
495	19.06.	Reservoir	56	835	1.56	47	1778	1935
403A	20.06.	River	70	1057	1.89	51	1949	2937
493A	20.06.	Reservoir	70	1057	1.89	42	12960	14123
423A	20.06.	River	57	851	1.53	22	6469	5875
442A	22.06.	River	73	1105	1.81	41	785	1344
455A	24.06.	River	53.5	795	1.64	52	641	932
464A	25.06.	River	69	1041	1.92	48	6468	2014
473A	27.06.	River	63	946	1.37	51	609	902
485A	03.07.	Reservoir	68	1025	1.95	45	2658	3824
413A	04.07.	River	58	866	1.50	48	1250	1677

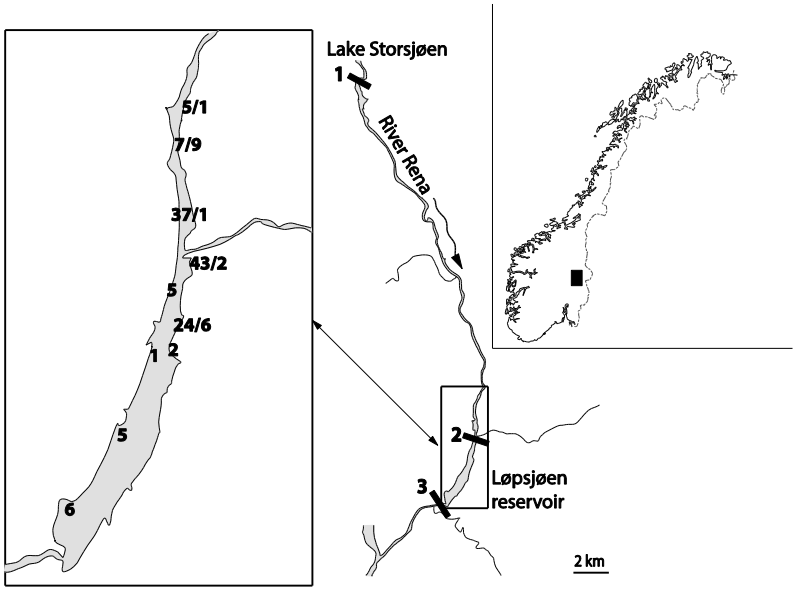


Figure 1 The location of River Rena and the Løpsjøen reservoir in southeastern Norway. Central panel: 1: the Storsjø dam (upper barrier to pike movement), 2: transition between reservoir and fast flowing river habitat, 3: the Løpsjø dam (lower barrier). Left panel: Detail of the Løpsjøen reservoir and the lower part of River Rena. Combined numbers (x/y) indicate tagging site and number of tagged fish: Floy tags (x) and radio tags (y). Single numbers indicate tagging sites of additional Floy tagged fish. The border between reservoir and river are immediately above the numbers 43/2.

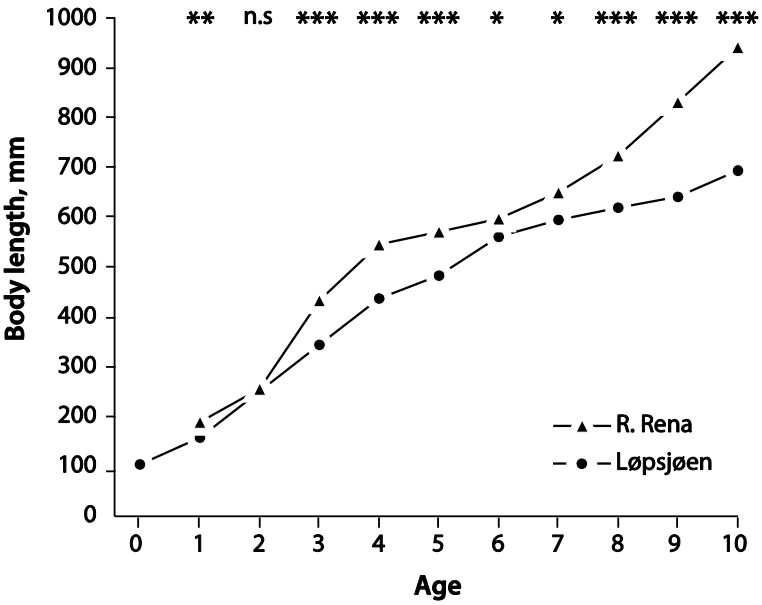
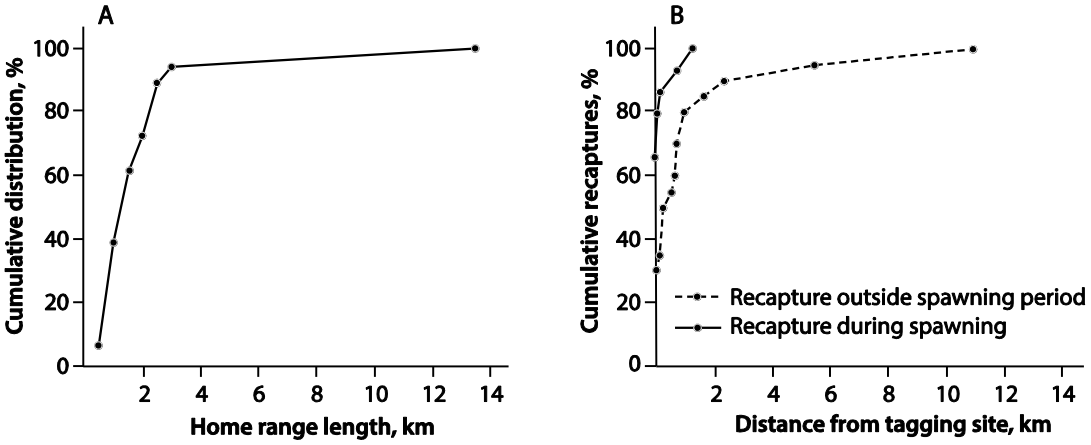


Figure 2 Length at age for northern pike from River Rena and the Løpsjøen reservoir, and the level of significance in pairwise t-tests of mean lengths (***: $p<0.001$; **: $p<0.01$; *: $p<0.05$; n.s.: $p>0.05$). Total number of fish analyzed: 280. The fish caught May-September during 2003-2004, 2007-2009 and 2011 were pooled.



528

529 Figure 3 A: Cumulative number of fish vs. maximum distances moved from tagging site (home range)
530 recorded for 19 radiotagged northern pike in River Rena and the Løpsjøen reservoir. B: Cumulative
531 number of fish vs. distance from tagging site of recaptures of Floy tagged northern pike, during the
532 next year spawning period, and outside of the spawning period.

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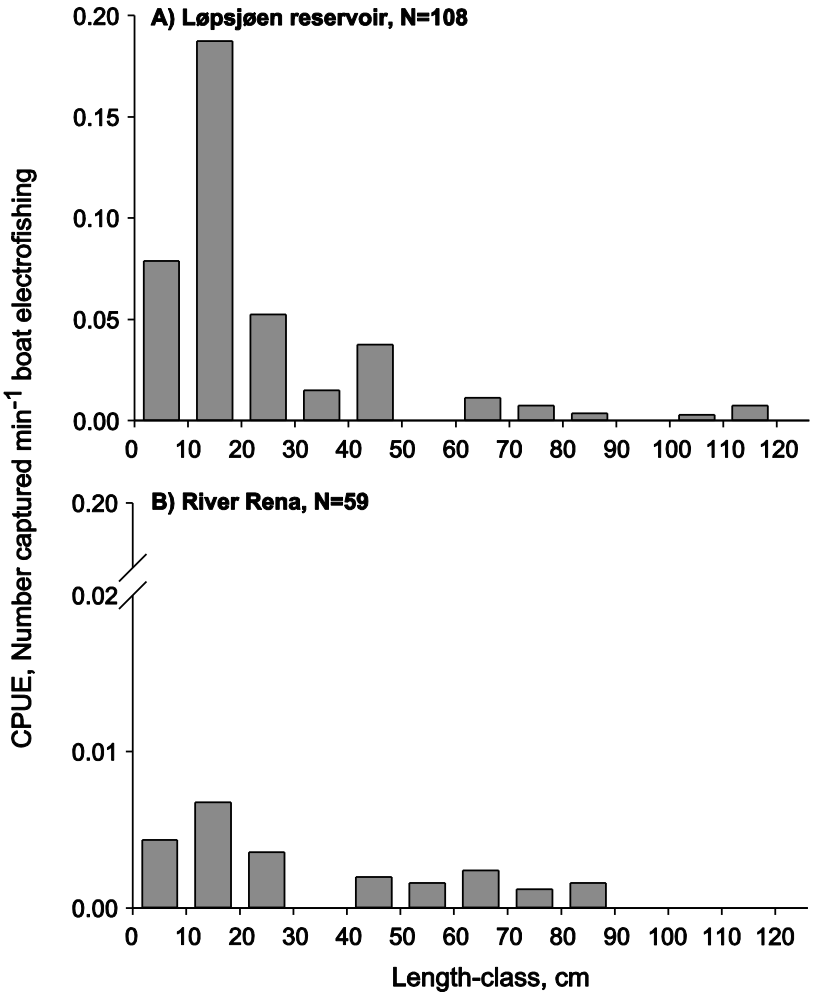


534

535 Figure 4 Length distribution of pike caught by boat electrofishing in the Løpsjøen reservoir (A) and
536 River Rena (B) 2008-2013. N = number of fish caught.

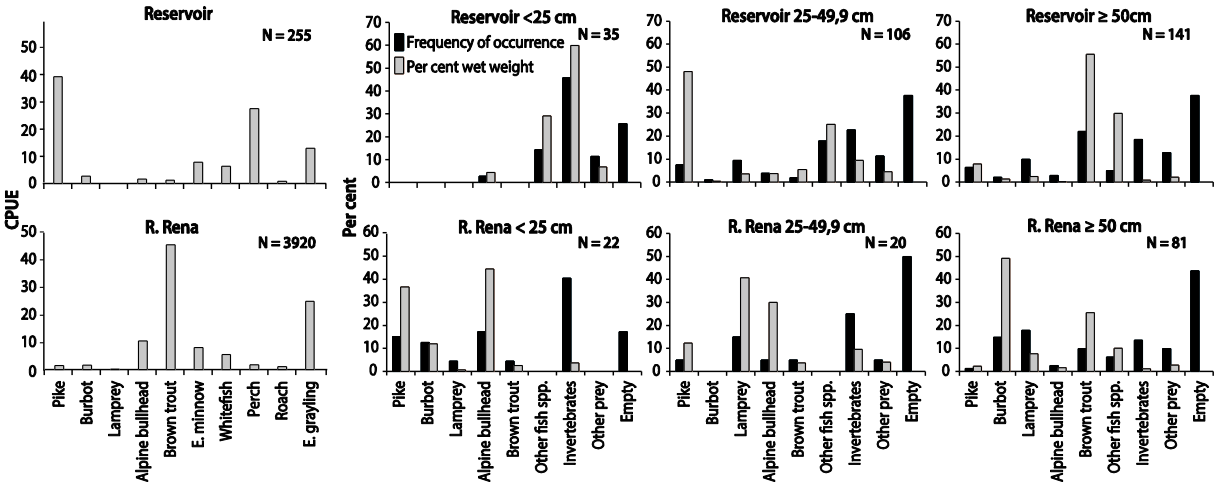


Figure 5 Diet of three length groups of northern pike in River Rena and the Løpsjøen reservoir (2003-2011, see text), and the proportion of different fish species captured during boat electrofishing in River Rena (2008 – 2012) and the Løpsjøen reservoir (2010-2012). Data were pooled from all sampling rounds. The representation of prey items is shown as frequency of occurrence in stomachs, and per cent wet weight of total stomach content of the combined sample. Boat electrofishing results are proportion of total catch.

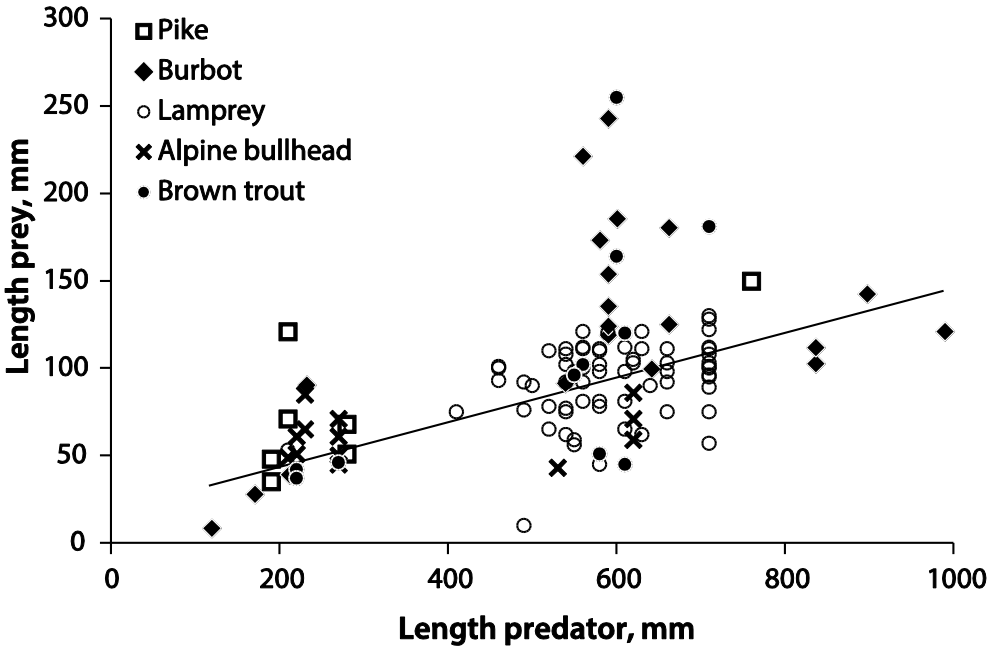
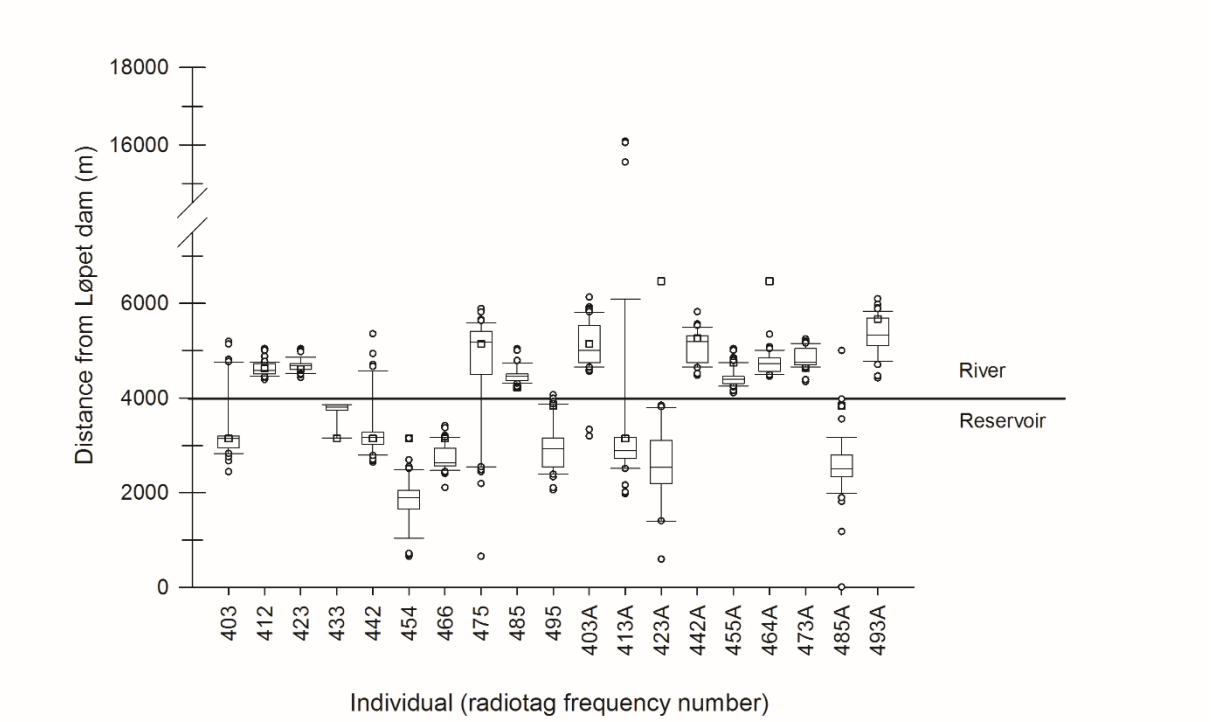


Figure 6 Prey length vs. predator length of identifiable and measurable prey in stomachs of pike caught in River Rena and the Løpsjøen reservoir. In a linear regression model, predator length explained only 21% of the variation in prey length ($L_{prey} = 0.11\ L_{pred} + 30.99$, $R^2 = 0.21$, $N = 130$).



552

553 Appendix 1: Box- and whiskerplot of the individual positions of radio-tagged pike monitored in River
554 Rena and Løpsjøen reservoir, June 2003 – June 2004. The boxes include 50% of the observations,
555 and the vertical lines show the 10 (⊥) and 90 (┬) percentiles (● = positions outside this range, □ =
556 tagging site). The median is shown by the unbroken horisontal line within the boxes.

557