

Telemetry observations of predation and migration behaviour of brown trout (*Salmo trutta*) smolts negotiating an artificial lake

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Michael Schwinn^a, Henrik Baktoft^a, Kim Aarestrup^a, Martyn C. Lucas^b, Anders Koed^a

^a) National Institute of Aquatic Resources, Technical University of Denmark, Vejlsøvej 39, 8600 Silkeborg, Denmark

^b) Department of Biosciences, University of Durham, South Road, Durham DH1 3LE, UK

Correspondence to:

Anders Koed

E-Mail: ak@aqua.dtu.dk

Phone: +45 35 88 31 46

Running title: Telemetry observations of smolts negotiating an artificial lake

Abstract

Eutrophication of coastal areas as a consequence of the agricultural use of fertilizers is a widespread problem. The development of artificial lakes and constructed wetlands in nutrient rich rivers is a widely used management tool in the fight to decrease eutrophication. Juvenile salmonids that have to negotiate these lakes during their downstream migration to the sea are commonly subjected to high mortality due to increased predation pressure and delayed passage. In this study, we double-tagged 39 brown trout smolts with PIT and radio tags to gain further insight into predation rates and migration patterns during their passage of an artificial lake in a Danish lowland stream in the spring of 2016. Thirty-four of the tagged smolts, caught and released upstream, entered the lake, of which 22 (65 %) successfully exited the lake. Four smolts (12 %) returned upstream to the river. Three smolts were predated in the lake by two northern pike (*Esox lucius*). Three tags were recovered from the lake bottom and two disappeared out of the study area after a last detection in the lake. Tracking the smolts manually and by automatic listening stations showed highly erratic movement patterns during lake passage. Further, we observed long delays of up to 27 days after the smolts reached the river mouth and before they entered the sea, potentially due to low sea water temperature or due to the stocking of a large amount of hatchery-reared brown trout smolts. The results are discussed in the context of abiotic and biotic factors, that differed considerably in the year 2016 compared with previous years.

Keywords: Passive Integrated Transponder, Radio Telemetry, Downstream Migration, Artificial Lake, Brown trout, Survival

Introduction

Eutrophication in the coastal zone due to agricultural use of fertilizers is a widespread problem and can lead to harmful algae blooms (Anderson et al., 2002) and hypoxia (Breitburg, 2002) with dramatic consequences for the whole ecosystem. The establishment of wetlands and shallow lakes to reduce the load of nitrogen and phosphorus transported by streams to coastal waters is a widely used management tool in Denmark (Hoffmann and Baattrup-Pedersen, 2007; Windolf et al., 2016), Sweden (Arheimer and Pers, 2017), Finland (Laakso et al., 2016) as well as in other European countries and other continents (Vymazal, 2017).

Artificial lakes and impoundments such as hydropower reservoirs are known to cause high rates of mortality for downstream migrating juvenile salmonids, possibly exceeding 90 %, mainly due to predation (Jepsen et al., 1998, 2000; Olsson et al., 2001; Schwinn et al., 2017a). Predatory pressure is often elevated in these areas due to a combination of high abundance of predators such as Great cormorant (*Phalacrocorax carbo*), Grey heron (*Ardea cinerea*) and Northern pike (*Esox lucius*) in and around lentic waters and the extended exposure period of the smolts, which are delayed in their downstream migration (Ruggles, 1980; Hansen et al., 1984).

The downstream migration of salmonid smolts is believed to be a partly passive process, but with active positioning components (Svendsen et al., 2007) and a strong correlation between migration speed and water flow is often observed (Connor et al., 2003; Gauld et al., 2013; Smith et al., 2002). In circumstances where smolts have to traverse lentic waters with no unidirectional currents, they must actively negotiate the area and search for the outlet. Little is known about patterns of lake passage, for example how direct the smolts navigate to the outlet.

Passive integrated transponder (PIT) telemetry is now one of the most effective ways used to study fish migration and survival in streams (Cooke et al. 2012), due to the small tag size, theoretically indefinite lifetime and low costs. However, for studies of predation and migration patterns in less physically constrained habitats, it is less suited, because PIT tags are limited in detection range (typically less than 1.3 m) and manual traceability (Cooke et al. 2012, Aarestrup et al. 2017). Radio tags, on the contrary, can be tracked over long distances and pinpointed with sub-meter precision (Lucas and Baras, 2000; Kuechle & Kuechle 2012). Typical detection ranges of radio tags transmitting from freshwater exceed several hundred meters, but signal strength is influenced by water depth, conductivity, orientation and size of the tag and receiver antennas and landscape (Lucas and Baras, 2000). This enables researchers to identify potential predators while the tag is still in the digestive tract of the predator or excreted at a location the fish could not reach on its own, e.g. in a bird colony. Further, radio telemetry makes it possible to gain insight into individual migration routes through lakes in a higher resolution unlike a PIT telemetry setup with stationary antennas. Double tagging with both methods combines the advantages of these telemetry systems.

Previous PIT telemetry studies conducted in the Danish artificial lake Egå Engsø during the years 2009 - 2016 could only speculate on mechanisms behind high mortality and passage time (Schwinn et al., 2017a, 2017b). Therefore, to investigate predation rates and individual migration patterns of brown trout smolts in this system, we double-tagged 39 smolts with radio transmitters and PIT tags during the smolt run in 2016. Survival data of c. 1500 PIT tagged smolts in the same river system and season are available (Schwinn et al., 2017b) for comparison. Further, we discuss the fate of the fish and predation in relation to environmental variables and the apparent effects of double tagging.

Material and Methods

Study area

The study was conducted in the River Egå and the adjoining lake Egå Engsø located north of the city of Aarhus in Denmark (56°13' N, 10°13' E, Figure 1). This shallow lake was created in 2006 by stopping artificial drainage that led to land subsidence of the area and the building of a low embankment. It has a mean depth of 0.8 m and a surface area of 1.12 km². The River Egå has its source in Lake Geding, c. 10 km upstream of Egå Engsø and drains into the Bay of Aarhus 4.1 km downstream of the Lake. The distance between the inlet and the outlet of the lake is 1.4 km. Two islands located in the eastern and western area of the lake harbor ground-nesting black-headed gulls (*Chroicocephalus ridibundus*) colonies. The annual mean discharge of River Egå into the lake is 0.52 m³s⁻¹ and water retention time in the lake is 21.9 d (governmental notice about the technical background for the aquatic environment plan for Aarhus Bight, 2011; <http://mst.dk/media/122347/17-arhusbugt-tekbaggrund011010.pdf>, in Danish).

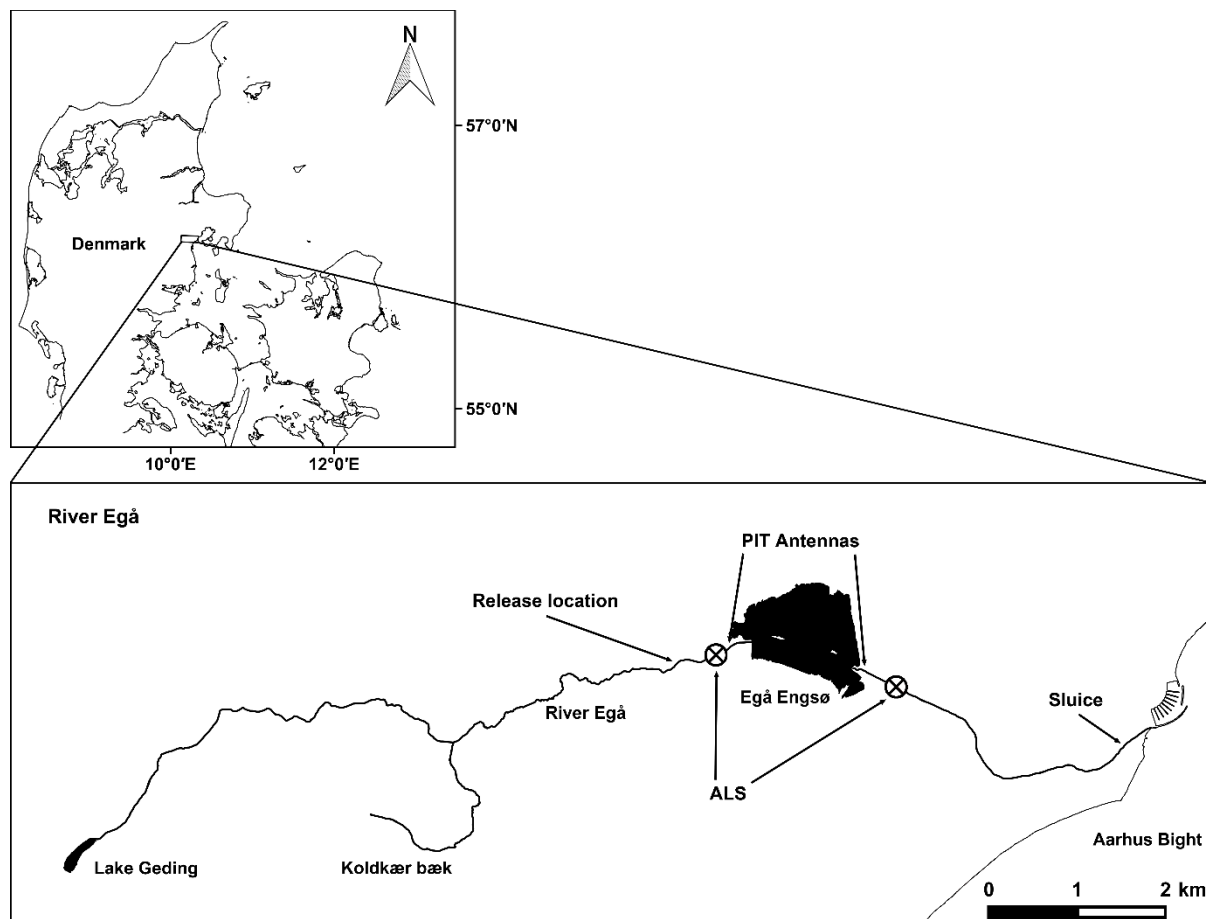


Figure 1: Map of the study area. Locations of automatic listening radio stations (ALS) are indicated by crossed circles.

Tagging procedure and radio telemetry

On 4 April 2016, 39 wild brown trout were caught by electrofishing in a 1.6 km stretch upstream of the PIT antenna at the inlet. The individuals appeared to be fully smoltified based on morphological criteria (i.e. distinct silvery body color, body shape and darkened fins). Their mean length was 17.7 (SD $\pm$ 1.9) cm and mean weight was 52.7 (SD $\pm$ 20.3) g. Fish were caught, tagged and released in two

groups. The first group consisting of 16 fish was caught in a 600 m stretch from upstream of the PIT antenna at the inlet to the release location, situated one km upstream of the inlet (Figure 1). The remaining 23 fish were caught in a 1 km stretch upstream of the release location.

Before surgery, fork length (FL) (± 1 mm) and weight (± 0.1 g) were measured. The tagging surgeries were performed following the protocol given by Koed et al., 2006, using absorbable sutures (Vicryl 4-0 FS-2, Ethicon, USA) and benzocaine (20 mgL^{-1}) as anesthetic. Radio transmitters (Model F1420, 142 MHz, Advanced Telemetry Systems, USA; dimensions: 16 mm length, 8 mm width, 7 mm height; weight: 1.3 g in air, expected lifetime: 39 d, pulse rate: 35 pulses per minute, pulse width: 20 ms) were surgically implanted in the peritoneal body cavity of smolts with a minimum FL of 15.7 cm. In this process, an 8 - 10 mm mid-ventral incision, posterior to the pelvic girdle was made using a scalpel and the antenna of the tag was run through a hole from the body cavity, pierced with a blunt needle. The trailing antenna of each tag was cut so it does not exceed the caudal fin to lower the risk of entanglement. Additionally, a PIT tag (Type RI-TRP-RRHP, Texas Instruments, USA; half duplex, 134 kHz, length 23 mm, diameter 3.85 mm, weight 0.6 g in air) was implanted in the peritoneal body cavity through the same opening. The incision was closed with two or three separate surgical sutures. The mean tag: body mass ratio was 3.9 %. Fish were released in two groups at 12:18 ($N = 16$) and 16:20 ($N = 23$). All fish re-gained full equilibrium and were swimming normally before release.

Two solar- and battery-powered automatic listening radio stations (ALS; Model SRX400, Lotek Wireless, Canada) connected to 9-element Yagi antennas were positioned ca. 400 m upstream of the inlet and 700 m downstream of the outlet of the lake. The receivers were programmed to cycle through all 39 frequencies in 3-second intervals without a timeout on signal acquisition, resulting in a 117-second cycle time. A range test was conducted before the study to confirm that the ALS did not register signals from radio tags in the lake. The upstream ALS operated continuously during the study period (4 April to 30 May 2016). The downstream ALS registered the last signal on 12 April 2016 and could not operate further due to vandalism. Two arrays of paired swim-through PIT antennas covering the entire streambed and channel depth, installed in 2009, operated at the inlet and outlet (300 m upstream and 20 m downstream of the lake) to register fish entering and leaving the lake. When energized, the PIT tag transmits its unique identification number that is stored together with the time and date of the registration. Each antenna had a detection range of approximately 0.5 m and operated with a 50 ms energization, 50 ms receiving time, resulting in a rate of ~ 10 scans per second. The stations are mains-powered and operated continuously during the study period. This was validated using timed auto-emitter check tags that register in 30-minute intervals on each individual antenna.

Manual radio tracking from land using a radio receiver (Model R2000, Advanced Telemetry Systems, USA) connected to a four-element Yagi antenna was performed on 34 days from 5 April to 30 May 2016, employing triangulation to estimate the location of each tag detected. Manual radio tracking from a boat in the lake was limited to fewer dates (12, 14, 28 April and 4, 17 and 30 May) to keep the disturbance of nesting black-headed gulls in the study area at minimum. Tracking by boat pinpointed radio tags using 'zero-point location' in which the gain is progressively reduced while homing in on the tag, until a short-range but even strength signal is obtained omnidirectionally, such that the boat is above or very close (< 2 m) to the tag (Cooke et al., 2012). On 20 April electrofishing was conducted near the outlet of the river to investigate the fate of the fish that left the lake but remained stationary close to the mouth of the river. On 12 and 29 April electrofishing was conducted to clarify the fate of transmitters in the lake. On 2 May two grey heron (*Ardea cinerea*) colonies, 10 and 20 km distant from the lake, were visited to track radio signals from transmitters of predated smolts. On 10 and 17 May electrofishing was conducted upstream of and in the lake, respectively, to investigate the fate of the fish. The radio telemetry study was terminated on 30 May, when the

smoltrun in Denmark typically ends (Rasmussen, 1986). On 21 June, the ground area of the heron colonies was scanned again using a pole-mounted PIT detector.

Monitoring of environmental variables

Water temperature at the upstream PIT station was measured at hourly intervals using a temperature logger (HOBO TidbiT v2, Onset, USA). Sea water temperatures were provided by a station in the marina in close proximity to the river mouth. Water level as a proxy of discharge was provided from a station 250 m upstream of the inlet at 15-minute intervals. Wind speed and direction data, recorded at hourly intervals at a weather station c. 10 km distant from the lake, were provided by the Danish Meteorological Institute. The zonal velocity, i.e. the component of the horizontal wind towards east was calculated using the formula: $u = -wind\ speed * \sin(dir * rad)$, where dir is the direction of the wind in respect to true north that the wind is coming from.

Results

Summary of the fate of the fish

In total, 34 out of 39 tagged fish entered Egå Engsø. Twenty two of the 34 lake entrants (64.7 %) were manually or automatically (by PIT antennas and/or ALS) tracked downstream of the lake, reflecting successful lake passage. Four of the remaining 12 lake entrant fish returned upstream. Three smolts were predated by northern pike (*Esox lucius*) in the lake. Three tags were recovered from the lake bottom. Two tags disappeared out of the study area after a last detection in the lake. Details about the fate of the tagged fish are given in Table 1.

Table 1. Length, weight and fate of the experimental fish

Frequency (MHz)	Length (cm)	Weight (g)	Fate
142.002	17.8	50.3	River mouth/Sea
142.013	18.2	55.3	River mouth/Sea
142.023	16.6	44	River mouth/Sea
142.033	16.3	44	River mouth/Sea
142.043	18.3	55.1	Predated by a pike (2.0 kg, 66 cm), retrieved by electro-fishing south of the outlet on 12 April.
142.051	18.8	58.9	Registered at upstream PIT station on 23 May, located at the south west shoreline of the lake on 24 May. Tag recovered from sediment at the inlet on 30 May. Probably predated.
142.061	18.2	63.1	River mouth/Sea
142.07	24.5	132.8	Last upstream registration at the ALS 23 April. Triangulated north west in the lake on 27 April. Disappeared out of study area after that, probably predated by a bird.
142.083	17.2	49.8	Tag triangulated on the western island on 20 April and remained stationary afterwards. Was detected at the river mouth between 11 and 19 April. Probably predated by a bird.
142.091	22.6	115.1	Tag recovered from the lake close to the outlet on 11 May, latest upstream location on 23 April. Recorded downstream near the outlet on 2 May. Probably predated.
142.102	16.3	38.1	Predated by pike (3.5 kg, 78 cm), retrieved by electrofishing on 29 April south of the outlet.

142.112	20.2	74.7	Remained upstream of the lake, latest location 24 May.
142.121	18.5	57.8	Registered at the outlet PIT and ALS two days after release. Last located near the outlet on 08 April. Probably reached the sea.
142.131	18.3	50.3	Remained upstream of the lake, latest location 24 May.
142.141	15.7	38.5	Probably in the sea: Registered on 06 April at the downstream ALS (but not downstream PIT station).
142.15	19.3	68.5	River mouth/Sea
142.16	17.3	44.6	Tag recovered on 30 May in the lake, 125 m south of the outlet. Located on several positions in the lake, indicating several back and forth movements between the inlet and outlet regions. Probably predated.
142.172	19.9	82.1	River mouth/Sea
142.181	17.7	42.8	Predated by pike (3.5 kg, 78 cm), retrieved by electrofishing on 29 April south of the outlet.
142.191	16.9	47	River mouth/Sea
142.211	20.2	69.2	Disappeared from the study area after being located near the upstream PIT station on 05 April. PIT tag found in a heron colony, 20km distant from the study site on 21.06.
142.221	16.1	40	Last detected 17 April in the north-eastern region of the lake. Probably predated by a bird.
142.231	15.7	39.1	River mouth/Sea
142.241	16.5	40.8	River mouth/Sea
142.251	16.1	37.8	Last detected on 10 April between the PIT antennas at the outlet. Probably reached the sea.
142.261	16.6	41.7	Remained upstream of the lake, last pinpointed on 12 May ca. 1000 m upstream of the release location.
142.272	17.9	53.3	Remained upstream of the lake, latest location on 23 April.
142.282	16.8	43.4	Located in the lake near the inlet on 08 April. Returned and remained upstream. Transmitter recovered on 17 May, 200 m upstream of the inlet, stationary since 10 April. Probably predated.
142.293	16.3	42.2	Remained upstream of the lake, latest location 27 April.
142.301	17.4	50.3	Tag recovered on 19 May in the outlet of the lake (shed tag).
142.311	19.7	65.4	River mouth/Sea
142.322	16.3	38.8	River mouth/Sea
142.332	17.4	46.5	Tag recovered on 17 May on the eastern shore of the lake, ca. 100m north of the outlet. Probably predated.
142.342	17.3	38.2	River mouth/Sea
142.352	16.8	41.3	River mouth/Sea
142.362	16	39.7	River mouth/Sea
142.371	16.3	40.7	Latest upstream PIT detection 20 May. Located close to the outlet on 17 May. Remained upstream after that, was recaptured 01.03.2017 50 m upstream of the PIT station at the inlet (211 mm length, 68.0 g weight)
142.381	16.2	36.6	River mouth/Sea
142.392	15.7	38.8	River mouth/Sea

Detection efficiency

The upstream PIT antennas and ALS registered 26 and 25 fish (76.5 % and 73.5 % of tagged fish known to have passed this locality), respectively. Combined, 33 unique tagged fish (97.1 %) were automatically detected upstream of the lake. One fish (2.9 %) that was detected downstream of the

lake was not detected at the upstream loggers. The downstream PIT antennas and ALS registered 15 and 14 fish (68.2 % and 63.6 % of tagged fish known to have passed through this locality), respectively. Eighteen unique fish (81.8 %) in total were automatically detected downstream of the lake. Four unique fish (18.2 %) were only manually detected downstream of the lake. Hence, double-tagging smolts increased detection rates by up to 23.6% at the upstream stations and 18.2% at the downstream stations, compared to detection rates of radio-tags tags alone. Compared to PIT tags alone, double-tagging increased detection rates by up to 20.6% at the upstream stations and 13.6% at the downstream station.

Predation

Predation by pike in the lake was confirmed for three smolts. One pike predated two of the radio tagged fish. Another pike had predated one radio tagged smolt. Radio transmitters of another four smolts were recovered from the bottom of the lake (three) and from the inlet (one), potentially as a result of predation. Yet those tags could be expelled by the fish or ended up on the bottom as a result of fish death. Therefore, pike predation is estimated to have caused the mortality of 3 - 6 smolts in the lake, without counting the tag found in the inlet.

Predation by birds during lake passage could not be verified in this study. Two smolts however were likely predated by birds as they disappeared out of the study area after a last registration in the lake. Bird predation is consequently estimated to have caused the death of 0 – 2 smolts in the lake. No radio signals were received during tracking in the heron colonies. One PIT tag (but not the corresponding radio tag) was found in a heron colony, 20 km from the study site, where a large amount of excreted PIT tags used in previous years in the study area were also detected (Schwinn, unpublished data), but this smolt was never registered in the lake. One tag appeared on the western island of the lake after the fish successfully traversed the lake and was tracked at the river mouth. It is highly likely that the smolt was predated by a bird at the river mouth and the transmitter defecated on the island.

In total, 9 out of 34 smolts (26.5 %) that entered the lake are assumed to be preyed upon during lake passage (8) or downstream of the lake (1). This is under the assumptions of no tag failure, no unrecorded tag shedding, and no tag loss following the death of any non-predated smolts.

Lake passage

Based on ALS and PIT registrations, lake passage time was calculated as the time difference between the first downstream registration and the latest previous upstream registration. Data are available for 15 fish. One fish (Frequency = 142.392 MHz) traversed the lake in 342.6 h. Mean lake passage time of the remaining 14 fish was 48.1 h (SD $\pm$ 29.2 h, range 4.1 - 99.2 h). Manual tracking showed highly erratic movement patterns of some of the smolts negotiating the lake. Examples are displayed in Figure 2. In several cases the fish returned to the western shore of the lake after having reached regions on the eastern shore, close to the outlet. Other fish were found near the northern shore of the lake after entering, far distant from the outlet. Lake entry occurred between 18.00 and 03.00, with two exceptions, and exit between 21.00 and 03.00 with one exception.

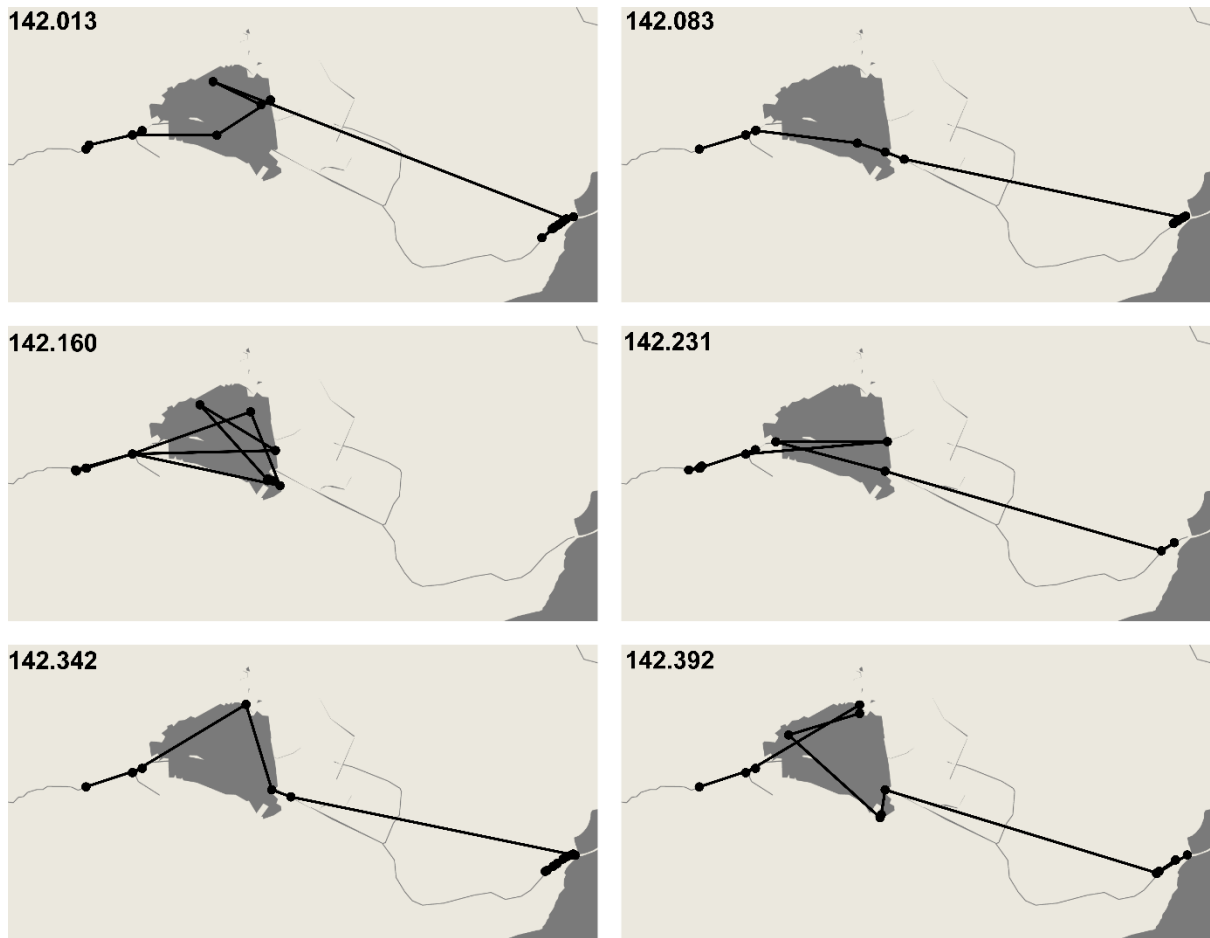


Figure 2: Example smolt tracks, illustrating the range of behavior observed. Consecutive manual and automatic registrations are connected with a line, showing movement patterns of smolts traversing the lake. Values in top right corner of panels refer to the radio-frequency identities of different smolts.

Environmental variables

During spring 2016, the river water temperature was mostly below 10° C until the end of April and water level was extremely high with two notable discharge peaks at the beginning and end of April. These conditions were atypical for the study area. Water temperature usually increases sooner, and water level remains lower (Schwinn et al., 2017b). Wind direction changed frequently between periods with dominants of easterly and westerly winds. With one exception, all successful fish entered and left the lake before 30 April, when water temperature was still low. Both peaks in discharge coincided with larger numbers of radio tagged fish entering and successfully leaving the lake (Fig. 3). Lake exit occurred often (16 out of 22 fish) in periods of westerly winds, i.e. winds blowing towards the outlet.

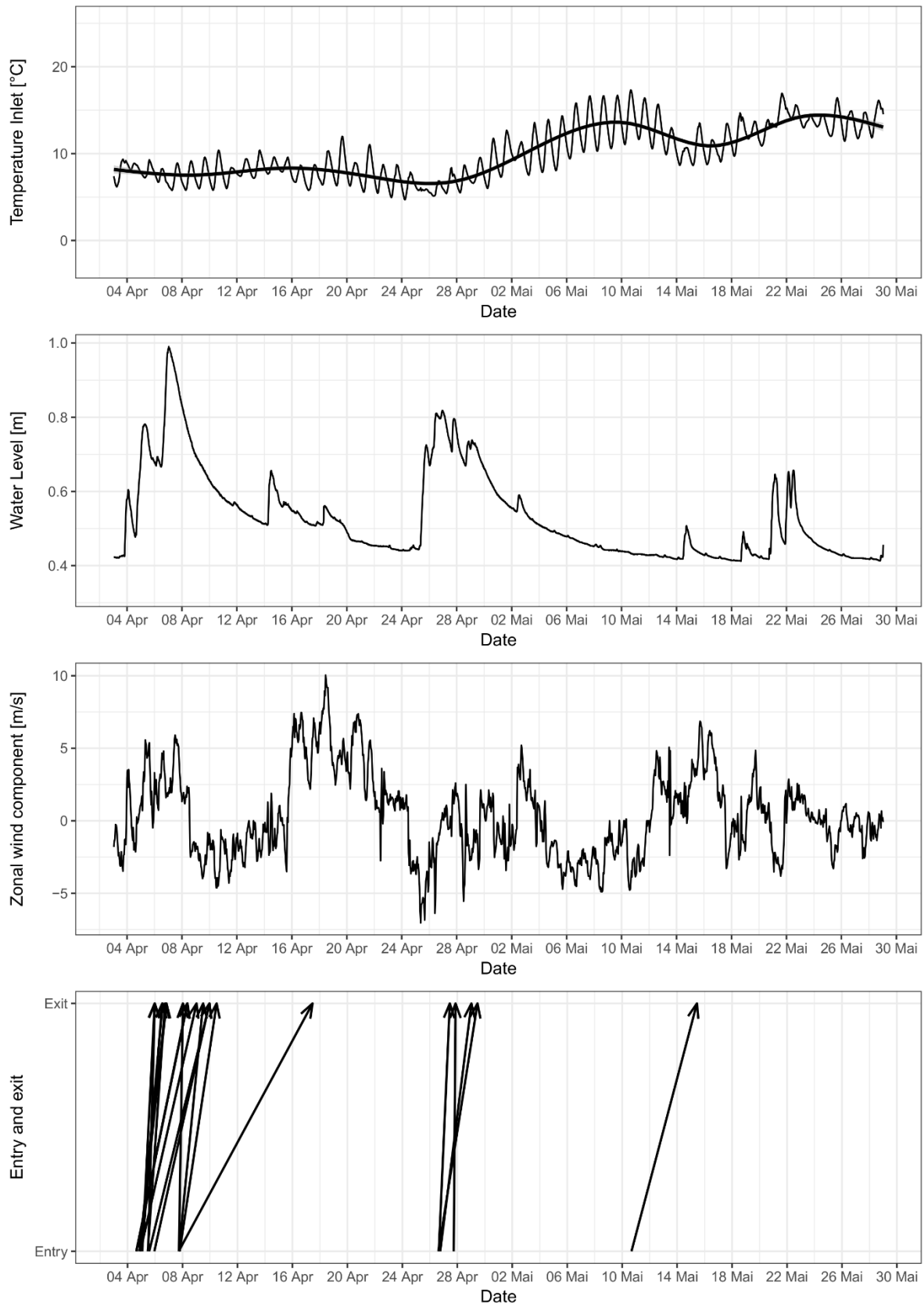


Figure 3: Environmental variables and lake entry/exit during the spring smolt run. Water temperature, water level at the inlet and east-west wind component are plotted against the date. Positive values of the zonal wind component are westerly wind components (blowing in the direction of the outlet). The bottom graph shows time of lake entry and exit for each fish that successfully negotiated the lake.

Sea entry

On 11 April, nine smolts were detected at the river mouth. Eight of those stayed in the river in close vicinity (< 450 m) to the river mouth for a period of 16 to 27 days. One transmitter was by triangulation estimated to be on the western island in the lake after eight days at the river mouth. Eight additional smolts arrived later at the river mouth, between 18 April and 1 May. Two of those spent 14 days there and the other six smolts stayed for 1-6 days. Most of the fish were not detected anymore after sea water temperature exceeded 9.1° C on 2 May.

Tagging Effects

Recaptured fish (N = 7) on 10 and 17 May, upstream of and in the lake, respectively, were examined. The incisions were generally healed, and most sutures were shed. One individual (Frequency = 142.301 MHz) showed clear signs of expulsion of the radio tag through the body wall (Jepsen et al., 2008, 2017). This particular tag was found in the outlet of the lake on 19 May. One individual was recaptured 400 m upstream of the inlet on 1 March 2017 by electrofishing. Its incision was fully healed, and the sutures were shed. There was no significant difference in tag: body mass ratio between the group that successfully negotiated the lake and the group that was assumed to be predated (unpaired t-test, two-tailed P-Value = 0.1979, t=1.3189, DF=28).

Discussion

In this study, we used a combination of radio- and PIT telemetry to study survival, migration routes, passage time and predation of brown trout smolts traversing an artificial lake. The combination of these methods enabled a better insight into individual movement patterns and predation, which PIT telemetry alone does not reveal.

Predation rate was lower than expected from survival estimates in previous years of PIT telemetry in the study area (Schwinn et al., 2017a). Predation by pike was shown for three smolts. Three additional transmitters were recovered from the lake bottom that were probably defecated or regurgitated by pike. But since these tags could potentially been expelled from smolts or ended up on the bottom due to mortality of the fish, there is an uncertainty in the estimation of predation rates. Northern pike are capable of consuming large amounts of smolts during the migration period (e.g. Kekäläinen et al., 2008, Sepulveda et al., 2015). Artificial waterbodies with low flow provide favorable habitat for pike and high predation rates by pike in those environments have been reported in other studies (Jepsen et al., 1998, 2000). Limiting factors of pike predation rates are turbid and humic water conditions that interfere with the visual range of the predator (Ranåker et al., 2012; Jönsson et al., 2013). Wind induced currents and discharge lead to high turbidity levels in Egå Engsø and eutrophication causes algal blooms in spring. That may explain the low observed number of tagged smolts eaten by northern pike in this study, that was conducted in a year with unusual high discharge (see below). Predation by birds in the lake could not be confirmed in this study, but the disappearing of two tags from the lake was likely caused by bird predation, since the reliability of the F1420 radio tag is very high and according to the manufacturer tag failure rates are less than 1%. The appearance of a transmitter on an island in the lake after it was tracked at the river mouth was also likely caused by bird predation. According to the database of the Danish Ornithological Society (dofbasen.dk) the number of observed cormorants during the study period was rather low compared to earlier years and the abundance of goosander (*Mergus merganser*), another smolt predator (Harris et al., 2008), was also low during the study period.

The overall survival of 65 % in 2016 greatly exceeded the estimated survival in previous years using PIT telemetry (mean 26% from 2009-2015, Schwinn et al., 2017a). However, environmental conditions in 2016 specifically favored high smolt survival. Survival of 259 PIT tagged wild smolts that entered the lake after 15 April in the same year was also high compared to previous years (49 %)

(Schwinn et al., 2017b). The mean discharge during the study period was 40 % higher compared with the years 2009-2015. Additionally, water temperatures were lower compared with previous years, all of which potentially favors successful lake passage directly or indirectly due to changes in predator occurrence and performance, turbidity and a lesser amount of fish desmolted (Schwinn et al., 2017a, 2017b). These atypical conditions that lead to high survival must be considered when drawing general conclusions about levels of predator-induced mortality, based on this particular smolt season.

The frequency of manual tracking from a boat was limited to minimize the disturbance of the bird colonies that breed on the lake's islands. This reduced the temporal resolution of records of fish traversing the lake. Eleven of the 22 fish that migrated through the lake were not manually located during their lake passage. However, triangulations and pinpoints done by manual tracking from land and boat respectively, as well as ALS and PIT detections revealed highly erratic movement patterns of fish traversing the lake. These movement patterns are conservative as movements between the detections remain unknown. However, in several cases the fish returned to the western shore of the lake after having reached regions on the eastern shore close to the outlet. Most of these reverse movements occurred under easterly wind conditions. Other fish were found near the northern shore of the lake after entering, ca. 1 km away from the outlet. In contrast, some fish were tracked in close proximity to the old streambed and possibly negotiated the lake in a more direct way. Overall, we could not observe a predominant pattern in the way the smolts traversed the lake. But our results clearly show that the smolts were delayed probably due to problems finding the outlet while actively roaming the lake. This delay extends the exposure of the fish to predators and can further lead to desmoltification, i.e. the fish lose their smolt characteristics, ability to survive in saltwater and their propensity to migrate (Handeland et al., 2013; McCormick et al., 1999; Stefansson et al., 1998). Lake exit often occurred (73 % of all occasions) under conditions of westerly winds, i.e. blowing in the direction of the outlet. Wind-induced currents provide the main flow in the lake and possibly facilitated lake exit for negotiating smolts when they were orientated towards the lake outlet. In this case, possible passive displacement towards the outlet would support active movements through the lake. Evidence from other studies also suggests that an active migration component is involved when salmonid smolts traverse lakes (Aarestrup et al., 1999; Bourgeois and O'Connell, 1988).

There was a substantial delay for the smolts upon arrival at the river mouth before sea entry. When sea water temperature exceeded a daily mean of 9.1° C the majority of smolts left the river mouth after being delayed for up to 27 days. Hvidsten et al. (1998) reported a close correlation between peaks of Atlantic salmon (*Salmo salar*) smolt migration when sea water temperatures reached 8° C in five Norwegian rivers recorded at traps in vicinity of the river mouth across a large latitudinal gradient. According to PIT data from 2016 (Schwinn et al., 2017b) the 50-percentile of smolt descent (defined as fish entering the lake) was reached on 9 April and sea water temperatures first surpassed 8° C on 10 April. However, after that sea water temperatures progressively fell (albeit with day-to-day fluctuations) until reaching a minimum of 5.5 °C on 27 April. From then on, sea water temperature continually rose up to 17° C on 12 May. Low sea water temperature reduces the osmoregulatory capacity of salmonid smolts (e.g. Finstad et al., 1988; Sigholt and Finstad, 1990; Arnesen et al., 1998). Consequently, the experimental fish potentially delayed sea entrance until their osmoregulatory capacity allowed them to tolerate present temperature and salinity conditions. Another reason for this delay could be the release of 21,800 1-year old hatchery-reared trout on 15 April. These fish might not have been fully smoltified when released and therefore delayed their sea entry. The radio tagged wild smolts potentially tried to form schools in this vast amount of hatchery-reared fish to minimize predation risk. The ultimate reason for the observed delay remains subject of speculation.

Double tagging smolts resulted in tag: body mass ratios of up to 5.2 % (mean: 3.9 %). In comparison to smolts in the same size range tagged with a PIT tag only and lake-entry over the same time period (Schwinn et al., 2017b) the current experimental fish exhibited higher survival (64.7 % vs 57.1 %) and faster lake passage (average of 48.1h, excluding the fish that negotiated the lake in 342.6 h vs 59.1h). Recaptured fish appeared to be in good health and without visible infections of the wounds. In one case, a fish was recaptured that was clearly in the process of expelling the tag through the body wall. This process is described in Jepsen et al., 2008 and consequences are rarely lethal. Based on these observations and on other studies that indicate that salmonids can be tagged with internal tags exceeding 5 % of the fish's total body mass with no or negligible effects on behaviour, growth and survival (Brown et al. 1999; Connors et al. 2002; Jepsen et al. 2005; Smircich and Kelly 2014), we assume that the effects of double tagging did not interfere with the results of this short-term study.

Conclusion

This study was conducted in a year with extraordinarily high survival of brown trout smolts negotiating the artificial lake Egå Engsø compared to previous years. Favorable environmental conditions such as high discharge, low temperatures, and westerly winds likely led to higher survival compared to other years. Based on our results for 2016, we estimate pike predation levels on smolts to have been 8.8 - 23.5 % of available smolts and avian predation levels to have been between 5.8 - 20.6 %. The combination of PIT and radio telemetry improved overall detection efficiency and provided enhanced information on smolt fate. It enabled us to follow the fish during the lake passage and revealed highly erratic, yet active migration patterns through the lake. Even though lake survival was higher compared to other years, the high smolt mortality compromises a self-sustaining anadromous brown trout population in the long run.

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