

EINAR KÄRGENBERG

Movement patterns of lithophilous
migratory fish in free-flowing and
fragmented rivers



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LIST OF ORIGINAL PUBLICATIONS

The current thesis was based on the following papers, which are referred to in the text by the Roman numerals **I–IV**:

- I** Tambets, M., Kärgerberg, E., Thorstad, E. B., Sandlund, O. T., Økland, F. & Thalfeldt, M. (2018). Effects of a dispersal barrier on freshwater migration of the vimba bream (*Vimba vimba*). *Boreal Environment Research*, 23: 339–353.
- II** Kärgerberg, E., Thorstad, E. B., Järvekülg, R., Sandlund, O. T., Saadre, E., Økland, F., Thalfeldt, M. & Tambets, M. (2020). Behaviour and mortality of downstream migrating Atlantic salmon smolts at a small power station with multiple migration routes. *Fisheries Management and Ecology*, 27(1), 32–40.
- III** Kärgerberg, E., Økland, F., Thalfeldt, M., Thorstad, E. B., Sandlund, O. T. & Tambets, M. (2020). Migration patterns of a potamodromous piscivore, asp (*Leuciscus aspius*), in a river-lake system. *Journal of Fish Biology*, 97(4), 996–1008.
- IV** Kärgerberg, E., Sandlund, O. T., Økland, F., Thalfeldt, M., Thorstad, E. B. & Tambets, M. Annual and diurnal activity cycles of a northern population of the large predatory cyprinid fish asp (*Leuciscus aspius*). Submitted manuscript.

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Author’s contribution to the studies (* denotes a moderate contribution, ** a high contribution, *** a leading role).

	I	II	III	IV
Designing of experiments and field studies	**	***	*	*
Database creation	***	***	***	***
Data analysis and interpretation	***	***	***	***
Drafting of manuscript	***	***	***	***
Final version	***	***	***	***

DEFINITIONS AND ABBREVIATIONS

- Anadromous:** Diadromous fishes which spend most of their lives in the sea, and which migrate into fresh waters to breed (McDowall, 1997)
- Batch-spawner:** Multiple spawning of an individual in a spawning season; a fish which sheds eggs more than once through a spawning season rather than within a short period (also called fractional spawner; FishBase Glossary, 2020)
- Diadromous:** Moving between saltwater and freshwater as part of its life cycle (Deinet *et al.*, 2020)
- Lithophilous:** Preferring mineral substrate, in fish reproduction – spawning on gravel, rocks (Balon, 1975)
- Migration:** Movements which result in an alternation between two or more separate habitats (i.e., a movement away from one habitat followed eventually by a return to it again) occurring with a regular periodicity (sometimes annual but certainly within the lifespan of an individual) and involving a large fraction of the population (Northcote, 1984)
- Migratory freshwater fish:** Any fish species classified as catadromous (migrates down rivers to the sea to spawn), anadromous, amphidromous (travels between freshwater and saltwater, but not to breed), diadromous or potamodromous (Deinet *et al.*, 2020)
- Natal fidelity:** A behaviour whereby an animal always returns to breed on the breeding ground where it originated (Horn, 2011)
- Parr:** A young salmonid (salmon or trout) with parr-marks (large oval spots on fish sides) before migration to the sea and after dispersal from the redd (a depression where the eggs are laid; FishBase Glossary, 2020)
- Phytophilous:** Preferring vegetation, in fish reproduction – spawning on plants (Balon, 1975)
- Potamodromous:** Fish species that migrates only between or within freshwater bodies to complete its life cycle (Deinet *et al.*, 2020)
- Semi-anadromous:** Species, populations or individuals that migrate between fresh and brackish water to spawn in freshwater. They do not enter waters with marine salinities (more than 30 ‰; Kottelat & Freyhof, 2007)
- Site fidelity:** The tendency to return to a previously occupied location (Switzer, 1993)
- Smolt:** Young salmonid which has developed silvery colouring on its sides, obscuring the parr marks, and which is about to migrate or has just migrated into the sea (FishBase Glossary, 2020)
- TL:** Total length, the length of the whole body between the most anterior and the most posterior points of the body (FishBase Glossary, 2020)

1. INTRODUCTION

More than half of living vertebrate species are fish and about half of them (near 18,000) spend the whole or a significant part of their life cycle in freshwaters (Helfman *et al.*, 2009; Fricke *et al.*, 2020). As freshwaters (mainly lakes and rivers) make up only about 0.01% of the water on Earth, it is evident that a disproportionately large fraction of the world's aquatic biodiversity resides in small areas. Most waterbodies and their catchments are in the focus of human activities (Brönmark & Hansson, 2002; Malmqvist & Rundle, 2002). Anthropogenic pressure on rivers and other freshwater systems has been increasing exponentially since World War II (Haidvogel, 2018). As a consequence, freshwater ecosystems and their biodiversity have become threatened (Best, 2019; He *et al.*, 2019; Tickner *et al.*, 2020).

Overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasion by exotic species are the main classical categories of threats to global freshwater biodiversity (Dudgeon *et al.*, 2006). The threat to freshwater fish fauna is most acute in the more developed regions (e.g. Europe) and areas suffering from extreme water stress (e.g. Western Asia; Darwall & Freyhof, 2016). Most European surface waters (60%) are not in good ecological status, among them rivers and transitional waters are in worse condition than lakes and coastal waters (Kristensen *et al.*, 2018). According to the European Red List of Freshwater Fishes (Freyhof & Brooks, 2011), 37% of all European freshwater fish species are threatened at a continental scale. Migratory freshwater fish are disproportionately more threatened compared to other fish groups (Deinet *et al.*, 2020). The Living Planet Index for describing migratory freshwater fish diversity (based on population trends) has declined between 1970–2016 in Europe by 93%, more than elsewhere (Deinet *et al.*, 2020).

Migratory freshwater fishes take advantage of long-distance movements (McIntyre *et al.*, 2016). Movement (an act of moving the body) is among the most important behavioural patterns of animals. For fish it allows response to physical and biological conditions and change between feeding, refuge (including wintering), and spawning habitats to increase their growth, survival, and reproductive success. These habitats may be located in the sea, lakes, slow-flowing or swift-flowing river sections, etc. Unfavourable movement conditions for fish between valuable habitats may lead to failure in completing their life cycle effectively. It may result in decline in fish population, phenotypic and genetic variation and overall viability (Tamario *et al.*, 2019; Thompson *et al.*, 2019; Vega-Retter *et al.*, 2020). Previous genetic variation as well ability for its recovery may be unknown (Thompson *et al.*, 2019). The highest vulnerability is connected to river and stream networks as the number of movement routes there are already naturally relatively limited and are progressively limited due to human encroachment and activities, but the need for opened migration routes for fish populations is inversely progressively more necessary. A typical disturbance on watercourses is the construction of infrastructure that forms barriers to fish migration and decreases

connectivity (Lucas & Baras, 2001). This leads to immediate negative impact on migratory fish species (Thieme *et al.*, 2010). Effective conservation of migratory fish requires both protection of various aquatic habitats and the connection routes between them.

Although slightly different definitions for migration exist (see e.g. Holden & Raitt, 1974; Northcote, 1984; Lucas & Baras, 2001; Dingle & Drake 2007; Thurow, 2016), it is generally described as a behavioural pattern, which consists of the regular, seasonal movements animals undertake between critical habitats to complete their life cycle (Dingle & Drake 2007; Deinet *et al.*, 2020). Migration in fish can be distinguished from other types of movement as it takes place between two or more well-separated habitats, occurs regularly (e.g. annually), involves a large proportion of a population, and is directed rather than random (Northcote, 1978). Many temperate freshwater fish species migrate regularly between freshwater and sea at particular stages of the life cycle (called diadromy; McDowall, 1997). Among them, catadromous fishes spawn in marine habitat, but (at least part of their populations) migrate to freshwater for feeding; anadromous fishes behave the opposite way to complete their life cycle. Similarly for diadromous fishes, the need for synchronised seasonal movements for survival may exist for fishes living completely in the freshwater (called potamodromous). Other freshwater-resident species may have stronger sedentary habits or their migratory behaviour is not well known (Lucas & Baras, 2001). Although habitat types important for fish species during their life are generally known, the migration patterns as well other movement rhythms remain largely unknown (e.g. for cyprinids).

Fish populations are especially vulnerable if they are migratory and depend on access to certain types of limited habitats. Many fishes are lithophilous (gravel-spawning) and – compared to other e.g. phytophilous fishes – their spawning areas are more threatened. For example, changes in water velocity, water level and gravel extraction may lead to siltation, drying up, or complete loss of gravelly spawning areas (Grabowski & Isely, 2007; Lucas & Baras, 2001). The scarceness of spawning habitat imposes additional constraints on lithophilous species (Lucas & Baras, 2001), especially in regions with relatively flat topography (e.g. Estonia). The situation may be even more complicated due to homing behaviour, as fish may need to access the same spawning area where they hatched (natal fidelity; Horn, 2011) or previously spawned (site fidelity; Switzer, 1993). Homing precision of salmonids is generally higher than for non-salmonids in temperate regions (Lucas & Baras, 2001), although relevant data for non-salmonids are scarce.

During recent centuries, the presence of barriers (such as weirs, dams and culverts) in rivers has grown immensely. To illustrate the global extent of human alteration of river flow, existing dams retain approximately 10 000 km³ of water, the equivalent of five times the volume of all the world's rivers (Nilsson & Berggren, 2000). Only 37% of rivers > 1,000 kilometres long remain free-flowing over their entire length; in addition, countless small dams exist worldwide (Grill *et al.*, 2019). Ongoing construction of dams on the most diverse and productive river systems in the world (e.g. in the Amazon basin), if completed, will trigger

massive hydrophysical and biotic disturbances (Grill *et al.*, 2015; Latrubesse *et al.*, 2017). It has been estimated at least 1.2 million instream barriers exist in European rivers (0.7 barriers km⁻¹), making Europe the world's most fragmented river landscape (Belletti *et al.*, 2020). In Estonia more than 1000 dams have been counted on watercourses; nearly 75% of them are impassable for fish, and about 40% have a significant impact on the state of fish, benthic fauna and flora (Envir, 2020). Changes in fish composition and abundance often reflect lost river continuity due to barriers. Relatively unfragmented rivers, still found in the Balkans, Scandinavia, the Baltic states, and parts of southern Europe, require urgent protection from new dam development (Belletti *et al.*, 2020).

Freshwater managers have remedied some of the negative consequences of barriers associated with fish passage. The best option for native fish assemblage is removal of the migration obstacle. Some alternative mitigation measures such as upstream transport of migrants (Backiel & Bontemps, 1996) or artificial propagation (Popovic *et al.*, 2013; Tański *et al.*, 2011), are time and effort consuming. Various types of fish passages have been designed. Fish passages must allow fish to migrate upstream as well as downstream without injuring fish or causing long delay (Larinier, 2001). As a rule, turbine channels and spillways (a structure for water controlled release) are not appropriate for that, although they may be attractive or even allow fish to pass in one direction (Larinier, 2001). All fishways may not be effective (Backiel & Penczak, 1989; Bunt *et al.*, 2012). Natural bypass channels are generally the best solutions as they are less selective than technical fish passes, which favour mainly salmonids (Larinier, 2002). Natural passages are excavated on the bank of the river and they mimic natural watercourses. Even such passages may function ineffectively (Larinier, 2002), and their functionality should be determined. Obstacles are often built for hydroelectricity purposes, and fish access to turbines should be prevented by using screens (bar racks) or other measures. The effectiveness of racks is questionable in situations when fish or other animals are physically able to pass them; racks may affect fish behaviour (Adam *et al.*, 2005). Turbine-induced mortality rates depend largely on turbine rotation speed and is higher for Francis type than Kaplan type (low head) turbines (Larinier, 2008). In addition to safe passage, it is important to consider that migrating rheophilic fish species depend on fast-flowing waters with appropriate habitat substrate. Loss of such areas may also significantly threaten stream and river ecosystem sustainability (Larinier, 2001; Birnie-Gauvin *et al.*, 2017).

The cyclical nature of fish activity and behaviour is fundamental. In most environments, fishes are diurnal and feed primarily during the day or they are nocturnal and feed by night (Reebs, 2002; Helfman *et al.*, 2009). Some feed mainly during crepuscular periods of twilight while only few show no periodicity (Reebs, 2002; Helfman *et al.*, 2009). Many circadian rhythms are under the control of endogenous molecular clocks (which persist even under constant light or darkness) and modulate most daily behavioral and physiological rhythms (Sánchez-Vázquez *et al.*, 2019). Activity rhythms can also be caused by changes in the water oxygen content or some other external factor (Lucas & Baras, 2001). In addition to diel periodicity, seasonal patterns in activity and distribution exist

in fish. At temperate latitudes, food and oxygen availability, vegetation cover, turbulence, and water clarity vary among seasons and determine fish movements between distinct habitats (Lucas & Baras, 2001; Helfman *et al.*, 2009). Fishes have optimal time and temperature range for reproduction, resulting in synchronization and periodicity in their movements.

Massive migrations of animals, including fish, have attracted people for a long time as they affect hunting possibilities or predict seasonal changes in the environment. Scientific study of fish migration has been carried out since at least the seventeenth century when ribbon tags were attached to the tails of juvenile Atlantic salmon *Salmo salar* to determine their growth and movements (Walton & Cotton, 2010). Tagging of fish (performed in Estonia since the 1920s; Riikoja, 1930) significantly enhanced our knowledge of fish movements. The main restriction of classical tagging methods is related to rather incidental recovery of tags and high mortality of recaptured fish.

Telemetry in freshwater environments began in the 1950s by developing miniature sonic tags to study the movements of individual adult salmon in relation to river dams (Trefethen, 1956). Wildlife tracking has become one of the most frequently employed approaches to monitor and study wildlife populations (Wittemyer *et al.*, 2019). Nowadays telemetry in aquatic environments uses a variety of electronic tags: acoustic and radio transmitters, data storage tags, pop-up satellite archival tags, and passive transponder tags (Thorstad *et al.*, 2013). Separately or especially in combination with other methods, telemetry gives an excellent opportunity to study in detail fish habitat use, movements between habitats and their timing, route choice, impact of habitat degradation and migration barriers or other installations, relation between movement parameters and environmental (e.g. temperature and discharge rate) or biological parameters, such as fish sex and size. As additional research is needed to improve our understanding of detailed movement behaviour and habitat use of migratory fish (Thurow, 2016), such opportunities are highly relevant. Acoustics is the most appropriate tracking technology in deep rivers, lakes and reservoirs (Lucas & Baras, 2001) and enables individual fish monitoring during all phases of day and year.

This thesis describes and analyses the results of the first studies of bony fish in Estonia which were conducted using acoustic telemetry. We studied smolts of Atlantic salmon (*Salmo salar*, **II**) and adults of two thermophilic cyprinids of Ponto-Caspian origin – asp (*Leuciscus aspius*, **III**, **IV**) and vimba bream (*Vimba vimba*, **I**). These species have small or diminished populations in Estonia but are potentially good targets for fishery. Their population decline is often related to migration obstacles (usually dams) preventing adults from reaching their spawning grounds and causing high mortality of descending juveniles. We hypothesized that salmon can benefit from nature-like fishways but encounter significant mortality during the smolt stage due to hydro-turbines and low effectiveness of bar racks. Next, we tested if vimba bream can still use historic spawning areas not available nowadays due to dams when released upstream from the migration obstacle. In an ecosystem with no obstacles for fish movement, migratory species

may have a wide variety of habitat use. It was tested when studying asp movements. There are general gaps in our knowledge of movement behaviour of cyprinids (Smith, 1991; Lucas & Baras, 2001; Marmulla, 2001). In our region, knowledge of seasonal and diel activity patterns of asp and vimba bream is poor and based mainly on old data (Erm *et al.*, 1970; Reeb, 2002; Lehtola *et al.*, 2006; Calles & Greenberg, 2007). Thus we hypothesized that movement and activity patterns not described earlier can be revealed for these species. Asp and vimba bream in Estonia live near the northern border of their distribution area, and our study describes behavioural response of cyprinids to potentially suboptimal thermal conditions.

Rivers Pärnu, Purtse and Emajõgi were selected due to their importance for migratory fish in Estonia (**I–IV**). The negative impact of the Sindi dam on R. Pärnu (**I**) on upstream migrating fish was the biggest in Estonia due to the relatively large size of the river, the proximity of the dam to the river mouth and the low functionality of the old fishway. In general, too little emphasis has been paid to downstream passage in fish studies (Silva *et al.*, 2018), which is also true in the Estonian context. Downstream passage was studied on R. Purtse (**II**) due to the importance of this river for salmonids. Salmon juveniles were used as they are physically able to pass bar racks protecting fish from hydropower infrastructures. Asp, a species under protection as well of exploitation interest, was studied in its top priority habitat in Estonia (Peipsi-Emajõgi-Võrtsjärv lake-river system) to fill gaps in knowledge of its movement behaviour and location of key habitats important for conservation, management and monitoring purposes (**III, IV**).

2. OBJECTIVES

The main objective of the present thesis was to investigate the movement behaviour of migratory lithophilous fish species in a riverine environment with open or disrupted movement conditions.

The specific objectives of the thesis were to:

- i) find out the effect of passable migration routes for fish (I–IV), particularly**
 - Would inaccessible spawning areas be used by vimba bream if migration were not obstructed by the dam (I)?
 - Is a natural type fishway with relatively small discharge preferred to alternative movement routes by descending Atlantic salmon smolts (II)?
 - Do fish populations with access to diverse habitats also have complex movement patterns (I, III, IV)?
- ii) quantify fish mortality during downstream migration at the power station with multiple migration routes (II)**
- iii) improve our knowledge of fish behaviour in relation to fish biological (size, age, sex) and habitat (water temperature and discharge and their trends, river section, movement direction and target) parameters (I–IV)**
- iv) reveal the annual and diel movement patterns of less studied migratory cyprinids (I, III, IV)**

3. MATERIALS AND METHODS

3.1 Study species

The vimba bream (**I**) is a riverine or semi-anadromous, batch-spawning cyprinid species, which inhabits mostly coastal zones and rivers in the Baltic (Gasiūnaitė *et al.*, 2008; Telesh *et al.*, 2008). The most important spawning river for the semi-anadromous vimba bream in Estonia is the R. Pärnu. The vimba bream is a target species for commercial fisheries, and in Estonian waters, the mean annual catches have decreased by two thirds during the last ninety years (Erm *et al.*, 2003; Eschbaum *et al.*, 2019). Semi-anadromous populations of the vimba bream have declined in most of its distribution area (Kottelat & Freyhof, 2007). As for other migrating fishes, the population decline is often related to hydropower dams and other barriers preventing upstream migration to reach spawning areas (Penczak *et al.*, 1998; Jurvelius & Auvinen, 2001).

Atlantic salmon (**II**) is a diadromous species with a high degree of fidelity to its natal rivers. The most profound impact on salmonid habitat availability is through hydropower development, man-made migration obstacles are common in rivers (HELCOM, 2011). Poor water quality has also severely reduced salmonid productions. After restoration measures, salmon presently reproduce regularly in ten (out of 12 historically known) Estonian rivers (ICES, 2018). Atlantic salmon has been included as “vulnerable” in the HELCOM Red List of Baltic Sea species and is listed in Annex II and V of the EU Habitat Directive (EEC, 1992; Kontula & Haldin, 2013).

The predatory cyprinid asp (**III, IV**) is a migratory potamodromous species inhabiting mainly the pelagic areas of large and medium-sized lowland rivers and lakes, and spawning in fast-flowing tributaries on gravel or submerged vegetation (Kottelat & Freyhof, 2007). It has been included as “near threatened” in the HELCOM Red List of Baltic Sea species and is listed in Annex II and V of the Habitat Directive (EEC, 1992; Kontula & Haldin, 2013). In Estonia, fishing for asp is prohibited as asp is protected by national legislation (RT, 2004). The habitats utilized by asp in Europe are in many cases protected as Natura 2000 areas. Present knowledge of the annual and diel movement patterns and utilization of habitats by asp is limited.

3.2 Study area

The present thesis is based on fish behavioural studies conducted in three river systems connected directly to the Baltic Sea or the large lakes Peipsi and Võrtsjärv (Fig. 1).

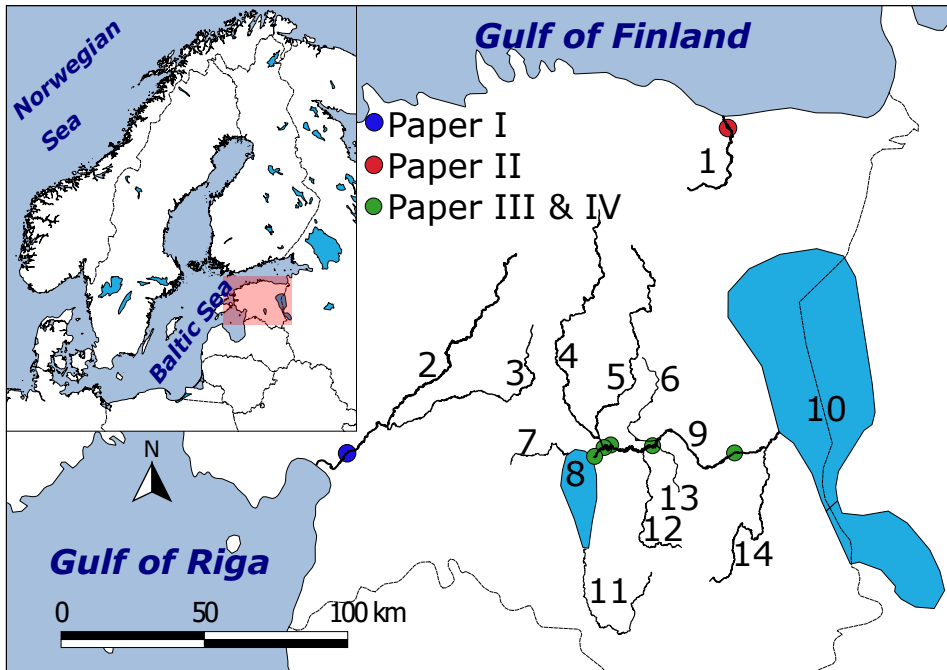


Figure 1. Study area and release sites of the tagged fish. 1 R. Purtse, 2 R. Pärnu, 3 R. Navesti, 4 R. Põltsamaa, 5 R. Pedja, 6 R. Laeva, 7 R. Tännassilma, 8 L. Võrtsjärv, 9 R. Emajõgi, 10 L. Peipsi, 11 R. Väike-Emajõgi, 12 R. Elva, 13 R. Ilmatsalu, 14 R. Ahja.

The 144 km long R. Pärnu (**I**) runs into the Gulf of Riga (Fig. 1). The 4.3 m high Sindi dam, created for industrial purposes, was situated 16 km upstream from the river mouth (the dam was demolished after this study), creating a 1.5 km long impounded stretch (reservoir) with slow-flowing water. The dam was an important obstacle. Its 70 m long vertical slot fish ladder had low functionality in the upstream direction (Erm, 1978; Anon., 2007; Wildlife Estonia, unpublished data). About 90% of the rapids potentially suitable for vimba bream spawning are situated upstream from the Sindi dam (Anon., 2007). The main spawning of the vimba bream occurred in two restricted rapid areas downstream from the dam.

The 51 km long R. Purtse (**II**) runs into the Gulf of Finland (Fig. 1). The river was historically one of the best salmon rivers in Estonia, but since the 1930s, salmon disappeared gradually due to pollution from oil shale mining (Mikelsaar, 1984). Since 2000, water quality has become suitable for salmonids (Kesler *et al.*, 2011), leading to modest but regular wild salmon reproduction (ICES, 2018). The Sillaoru Hydroelectric Plant complex was constructed 4.9 km from the river mouth with a 3.2 m high dam, and equipped with natural type fishway.

The 100 km long R. Emajõgi (**III, IV**) runs into L. Peipsi (3,555 km²) from L. Võrtsjärv (269 km², Fig. 1). The river has a mean annual water discharge of 70 m³ s⁻¹, a very low gradient (0.036 m km⁻¹) and varying depth (mean 3.4 m, max 10.7 m, Maritime Administration of Estonia, unpublished data). The upper 40 km reach of the river is intensively meandering. Most of the oxbow lakes, with

a total length of > 50 km, are situated in this area. The R. Emajõgi is free of obstacles or barriers to fish migration. There are few rapids in the river, restricted to short sections. Most rapids suitable for spawning of lithophilous fish are located in the tributaries. The rivers Pedja and Ahja are the biggest tributaries.

3.3 Fish and tagging

The present thesis is based on the behaviour of 575 fish (I–IV) which were marked externally (II–IV) and/or equipped in 122 cases with acoustic telemetry tags (I–IV). The fish were released into the three river systems during the years 2011–2015 (I–IV; Fig. 1).

Thirty adult vimba bream with mean total length (TL) 339 mm (range 300–405 mm) were captured for tagging on 14 and 15 May 2013, during spawning migration (I). The fish were caught in the R. Pärnu below the Sindi dam and in the downstream end of the Sindi dam fish ladder using electrofishing. The fish were anaesthetized on site, coded acoustic transmitters were implanted surgically (Vemco, Nova Scotia, Canada), and incisions were closed with two sutures. All the fish could hold position and swim normally after recovering for 3–6 minutes, and were then released into the Sindi reservoir, 50 m upstream from the dam.

Two-year-old fin-clipped Atlantic salmon smolts (491 specimen, II) were released on 14 May 2015 at a site 50 m upstream from the last rapid above the reservoir (0.6 km upstream from the Sillaoru dam). The fish were reared in the Põlula Hatchery. The mean TL of the smolts was 207 mm (range 145–256 mm). Thirty-eight smolts were tagged with individually coded acoustic transmitters (Thelma Biotel AS, Trondheim, Norway) 1.5–4.0 hours before release. Each smolt was anaesthetized immediately before surgery. The acoustic tags were implanted into the abdominal cavity through a 1.5 cm long ventral incision which was closed with two sutures. Tagged fish were transported to the release site together with fin-clipped smolts in a container with aerated water and a controlled oxygen level.

In total, 54 mature asp with mean TL 664 mm (range 490–810 mm) were caught with fyke-nets or gillnets in the upper, middle and lower third of R. Emajõgi (III, IV). Fish were caught between 10 October and 21 December, 2011 (N = 23) and between 3 and 28 April, 2012 (N = 31) and were tagged on site on the same day, or were transferred to keep net boxes for one to four days before tagging. The fish were anaesthetized on site and coded acoustic transmitters (Vemco, Nova Scotia) were surgically implanted into the body cavity. Incisions were closed with two sutures. After recovering for 2–6 minutes, all fish were able to hold position and swim normally, and were thereafter released into the river near the catch site.

3.4 Recording of fish tagged with acoustic transmitters

The movements of the tagged fish (I–IV) were monitored by using stationary Vemco VR2W automatic receivers and a mobile receiver VR100 for manual tracking (Vemco Ltd., Canada). The VR2W receivers detected and saved individual signal codes of acoustic transmitters as well as the date and time when fish were within their detection range. The information was stored by the receiver and later downloaded to a computer. In the R. Pärnu water-system (I), thirteen automatic receivers were deployed all together in the R. Pärnu and in the Navesti tributary. Manual tracking was conducted every fourth day by boat from 15 May to 11 June to locate tagged fish, covering the main spawning season of 2013. The length of the surveyed stretch was adjusted according to the data obtained from the automatic receivers.

In R. Purtse (II), six stationary Vemco VR2W automatic receivers were used. Manual tracking was performed in the reservoir and turbine channel at least once per day to locate salmon smolts and detect shorter movements, and four times at the release site.

In R. Emajõgi water-system (III, IV), receivers were deployed in R. Emajõgi and connected waterbodies. Nineteen receivers were deployed year-round for 2.5 years. An additional 19 locations were temporarily deployed with receivers, depending on seasons and fish locations (on average about 2.5 months per site). Manual tracking to locate tagged fish was performed 71 times by boat from 17 November 2011 to 10 April 2014, covering R. Emajõgi and tributaries, oxbow lakes and artificial waterbodies (gravel pits and boat channels). The river stretch covered by tracking was adjusted according to the data obtained from the automatic receivers. Tracking in lakes Peipsi and Võrtsjärv was restricted to areas near the river mouths.

3.5 Additional methods

To determine the timing and selected route of downstream migration of fin-clipped salmon smolts (II), the downstream end of all three migration routes through the hydropower complex was closed with fyke nets. The fyke nets entirely covered the migration route cross-sections. To monitor for possible delayed mortality, some of the seemingly uninjured smolts that descended through the turbines, or fishway and spillway (control group) were kept in separate keep net boxes, placed in a slowly running part of the river. These and several other techniques (diving, usage of D.C. fishing aggregates, evaluation of possible underestimation of dead fish) are described in paper II. To link fish behaviour on water parameters data from the hydrometric stations of Estonian Environment Agency were used (I–IV) and direct measurements with flow rate meter were carried out (II).

3.6 Data analyses

A database including more than one million location records of manual and stationary receivers were created. Statistical tests were performed using the R program (R Core Team, 2020; **I–IV**).

To test if the fish movement activity had a diel (**I, IV**), seasonal (**I**), annual or interannual (**IV**) pattern, the data were divided into periods of the day (dawn, day, dusk and night) and into seasons (**I**) or months (**IV**). Dawn and dusk periods were defined as ± 1 hour from the time when the sun's upper edge appeared or disappeared on the horizon (sunrise or sunset) according to local timetables (**I, IV**). The duration of day and night periods was calculated for each day when fish activity was detected by subtracting dawn and dusk periods (**I, IV**).

A vimba bream and asp 'movement activity' event (**I, IV**) was defined as the arrival or departure in any receiver's detection range. Detections within one hour since the last recording by the same receiver were excluded. All activity events during each day period were counted. The null hypothesis ("expected level") for diel activity was that the fish did not differ in the number of activity events between dawn, day, dusk and night, adjusted for day and night lengths (**I, IV**). The possible deviation from the null hypothesis was tested by Pearson's Chi-squared goodness-of-fit test for activity levels between night, dawn, day and dusk within each season (**I**) or month (**IV**).

To test the influence of diel period on movement direction (**I, IV**), the total number of upstream and downstream movements were counted for each diel period. Movements during these periods were counted and analyzed by Chi-squared test (**I, IV**). Division in more than two periods was not done as this would have reduced statistical power (**I**), but in **IV**, differences in activity between each four day period and the rest of the day was tested.

To identify fish 'movement speed', fish movement time was measured along the shortest possible path through the waterbody (**I, II, IV**). The range area of stationary receivers along the rivers upstream and downstream (typically until the nearest river meander) were subtracted from the distance moved by fish. Short distances were excluded to reduce possible inaccuracy in calculating movement speeds (**I, II, IV**).

Movement speed data was used to describe variation in asp seasonal activity (**IV**). To investigate how different environmental and biological parameters were related to fish movement speed, a linear mixed-effects model (LMM) was built, using the lmer function of the lme4 package in R (Bates *et al.*, 2020).

The relationship between asp movement speed and environmental variables (**IV**) was described in more detail by applying segmented regression analysis to examine if the relationship between movement speed and environmental variables deviated from a linear relation (Muggeo, 2020).

Wilcoxon Signed-Rank tests were used to test if movement speeds differed between river stretches with or without rapids and between upstream and downstream movements of vimba bream (**I**).

A Wald-Wolfowitz runs test was used to reveal if the sequence of descent to the sea was associated with gender of vimba bream (I).

A Chi-squared test of goodness-of-fit was used to identify if riverine and lacustrine habitats were utilized to a different extent by asp (III). The same test was also used to identify if the entering rate of fish to tributaries differed between the main feeding season and the remaining period (III).

To determine the main environmental drivers of asp first entering tributaries during the second half of the year (III), a binomial logistic generalized linear model (GLM) was used. GLM was used also to examine the probability of tagged asp individuals descending from the river to L. Peipsi (III).

Egon Pearson's $N - 1$ Chi-squared test (Campbell, 2007) was used to test whether the asp entering the tributaries for the spawning period to a larger extent moved between waterbodies during wintering time than the fish remaining in the main river for the spawning period (III).

To test whether there were differences in wintering areas between asp that stayed in R. Emajõgi during the spawning period or ascended to tributaries (rivers Põltsamaa and Pedja), a Welch two sample t-test was used (III).

Asp 'home range' was defined as the riverine distance between the extreme upstream and downstream locations during day, month or year (IV). 'Movement distance' was the cumulative sum of movement routes (IV) during a month or year, which were calculated the same way as described for movement speed, except that the range area of receivers was not subtracted.

The distribution of fish and water flow between different migratory routes past the power station (II) was tested with a Chi-squared test. Fin-clipped smolts and smolts tagged with acoustic transmitters were treated together as their distribution did not differ (Fisher's exact test).

To test whether there were differences in mean TL of smolts that descended through the turbine and smolts released in the river upstream of the hydropower complex (II), a Welch two sample t-test was used.

A Chi-squared test was used to test differences in delayed mortality between the turbine group and control group (II). The same test was used to test if the proportional share of smolts between the fishway and other routes differed between the first and subsequent days (II).

4. RESULTS AND DISCUSSION

4.1 Importance of opened migration routes for fish

4.1.1 Attractiveness of inaccessible spawning areas

In our study, about half of the vimba bream that were caught during their spawning migration in the R. Pärnu under the Sindi dam and released in the reservoir continued their upstream migration. The fish utilized all nearby upstream spawning areas, and several fish performed longer (> 24 km) migrations (I; Fig. 2).

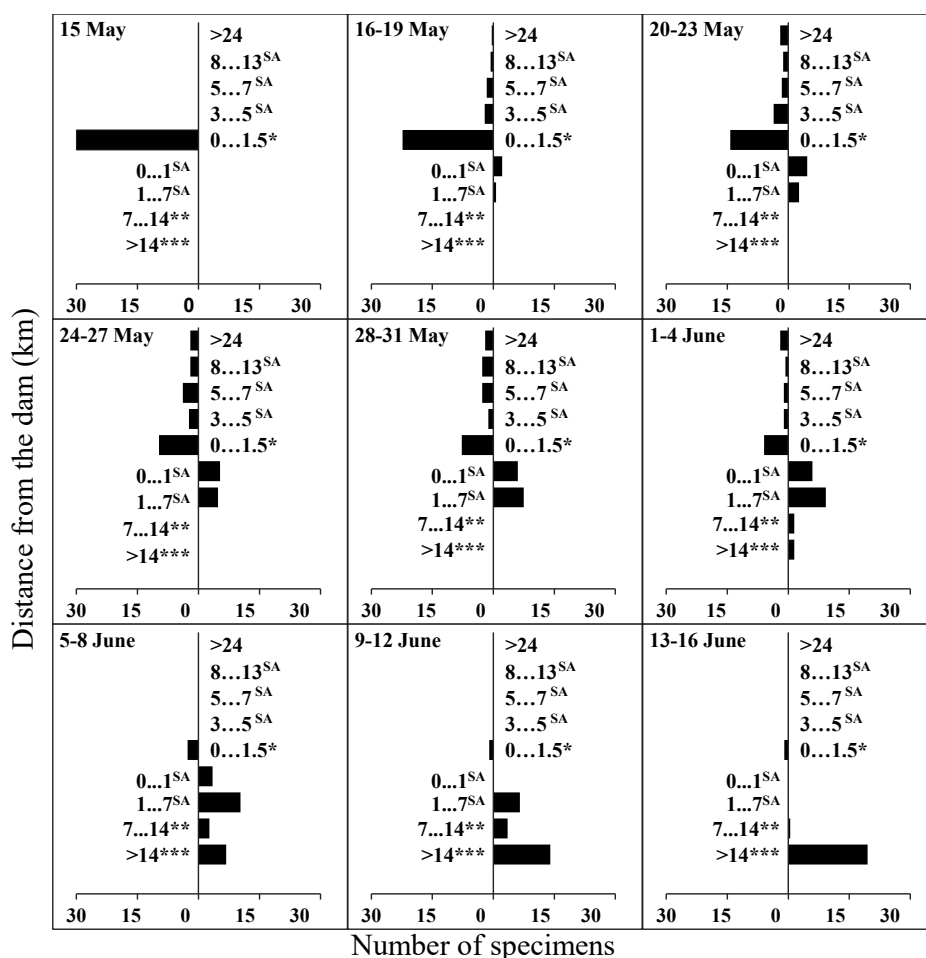


Figure 2. Habitat use by acoustically tagged vimba bream after release in the Sindi reservoir (R. Pärnu) on 15 May 2013. The distance of spawning areas (SA), the reservoir (*), a slow running river segment (**), the sea (***) and the lower part of the tributary Navesti (> 24) from the dam are shown on the vertical axis. Bars to the left indicate fish locations upstream and bars to the right downstream of the Sindi dam. Figure modified from I.

Fish that moved upstream from the Sindi reservoir, stayed in either one, two or three different spawning areas before returning downstream (see 4.4.1, Fig. 9). Some of them moved to upstream spawning areas a second time before returning downstream past the dam. Some fish from upstream areas moved directly from the dam to the sea, others stopped in one or two downstream spawning areas before descending to the sea (I).

State and attractiveness of habitats upstream are critical to consider while river connectivity is being restored (Larinier, 2001). Our results show that inaccessible spawning areas would be used by fish if migration were not obstructed by dams on R. Pärnu. Still, some vimba breams moved only downstream from the release site (I). Similar downstream movement behaviour has also been recorded for other species (e.g. *Prochilodus lineatus*) after transferring them upstream in the reservoir (Antonio *et al.*, 2007; De Fries *et al.*, 2019) and disorientation due to lentic environment has been suggested as a possible reason (Antonio *et al.*, 2007). It may be relevant to design fishway inflows near the more lotic river section to reduce the disorientation rate of upstream migrating fish.

After conducting this study, demolition of Sindi dam started (2018). For now, large parts of upstream spawning areas are available to anadromous fish. Earlier, ~90% of the rapids potentially suitable for vimba bream spawning were located upstream from the Sindi dam (Anon., 2007). The present situation in habitat usage rate and possible problems in river connectivity for vimba bream and other anadromous species (especially with weaker swimming abilities, e.g. river lamprey) in upstream areas should be quantified.

4.1.2 Attractiveness of a natural type fishway and alternative routes

Atlantic salmon smolts released upstream had to pass the 2.1 ha reservoir and find the entrance of a nature-like fishway on the downstream end of the reservoir. Two other downstream migration routes were the turbine channel and spillway. The turbine channel received about 80% of the water discharge, the rest was divided almost equally between the fishway and spillway (II; Fig. 3).

According to our results, out of 491 two-year-old Atlantic salmon smolts, 459 (94%) were detected descending past the power station, 74/71% descended through the fishway, 24/21% through the turbines, and 3/7% used the spillway (fin-clipped or acoustically tagged smolts, respectively; Fig. 3). According to receiver data, ~90% of the fish that passed the reservoir explored only one of the three possible exit routes. Fyke-net catches and observations during diving showed that 278 (62%) of the smolts passed the power station within the first 24 hours and 443 (90%) during the first three days. The proportional share of smolts between the fishway and other routes differed between the first and subsequent days (III). Most smolts used the natural type fishway, which can be attractive for descending fish despite the relatively small discharge supplied to the fishway. Previous studies have indicated that the proportion of smolts passing through a movement route depends largely on the proportion of water diverted through it

(Ruggles, 1980; Hvidsten & Johnsen, 1997; Serrano *et al.*, 2009). However, this seems not to be a rule (Havn *et al.*, 2017; Haraldstad *et al.*, 2018; **II**). Bypass efficiency may depend largely on small details (Haraldstad *et al.*, 2019), and thus every technical solution should be assessed separately (Calles & Greenberg, 2007).

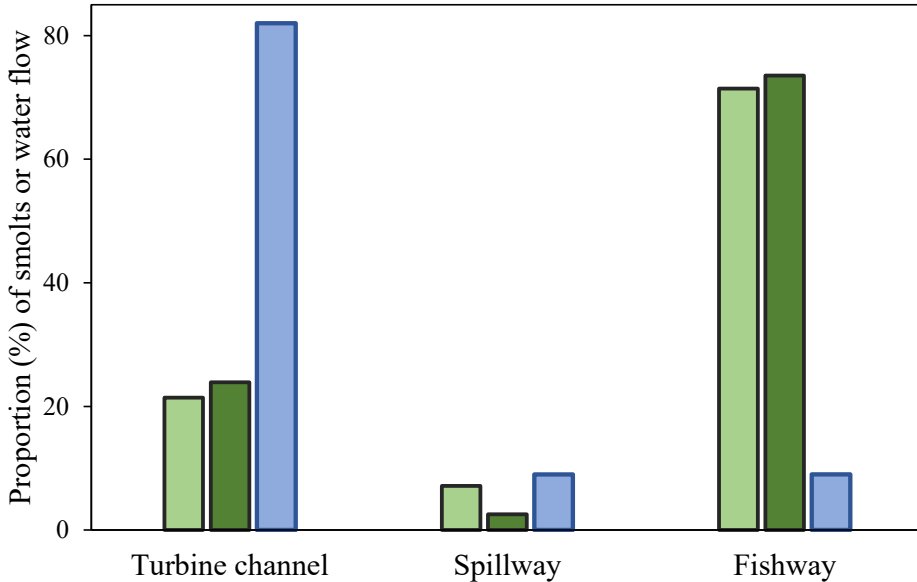


Figure 3. Proportion of salmon smolts (green bars) and total water flow (blue bars) moving through the different migration routes. Finclipped (N = 431, dark green) and smolts with acoustic transmitters (N = 28, light green) are presented separately. Figure modified from **II**.

As shown in study **II**, different types of man-made movement routes may be used by fish. Such routes may cause high mortality (e.g. turbines; Larinier, 2001). Still, if such routes are built favourably for fish, they may be used as safe bypasses (e.g. trash gates, floodgates; Haraldstad *et al.*, 2019). The spillway was not an efficient alternative as a bypass route in our study. Impact of hydraulic installations should be considered for fish, especially in situations in which such constructions interconnect valuable fish habitats and form alternative movement routes.

4.1.3 Relationship between behavioural diversity and habitat complexity

According to our study, asp population inhabiting the R. Emajõgi water system utilized feeding, spawning and wintering areas that existed each in 3–5 different waterbodies (see 4.4.1, Fig. 6). All the tagged fish utilised both lotic and lentic

environments (rivers, lakes, oxbow lakes) over the two-year study period. A variation in habitat use was detected during all seasons, including the spawning period, when fish were located in R. Emajõgi or in four different tributaries (III).

During each month (except February) the asp population moved inside or towards different lentic and lotic waterbodies (Table 1 in IV) as fish behaviour differed individually. For individual fish, the variation in habitat use throughout the year could include visits to one or both lakes, the main river, and one or more tributaries (III; Table 1), resulting in large yearly home ranges (minimum 40 km long river stretch, mean about 80 km, IV). Each year about 2/3 of the fish descended to L. Peipsi during the post-spawning and feeding periods (III). Some fish visited also (or only) L. Võrtsjärv or other waterbodies (III). The habitat use of the individuals was mostly very variable. The diversity among migration patterns and habitat use of the fish in our study area may be a consequence of the large number of available habitats. Large variation in habitat use by asp has also been described in the large R. Elbe system (Fredrich, 2003).

Vimba bream released upstream from the Sindi dam during their spawning migration stopped in up to four different spawning areas (I; see 4.4.1, Fig. 9). This could not be possible with the limited number of spawning areas (e.g. for fish remaining below the Sindi dam), which is typical for rivers with migration barriers relatively close to river mouths. Stopping for a period in more than one spawning area has also been reported for another riverine batch spawning species, chub *Leuciscus cephalus* (Fredrich *et al.*, 2003). The vimba bream has 2 or 3 egg batches (Lelek, 1987; Erm *et al.*, 2003). Batch spawning may raise individual fitness by increasing the genetic diversity of the offspring, and possibly reduce mortality rate due to different conditions at different sites and time. Such life histories spreading their reproductive risks are termed bet-hedging strategies (Childs *et al.*, 2010). For individuals of the same population, the diversity in timing of migrations and therefore also the number of life history strategies may be high (e.g. > 100 for Atlantic salmon) and successful management is needed to enable and conserve such variation (Erkinaro *et al.*, 2019). Maintaining population diversity is critical to stabilize ecosystem services and to secure the economies and livelihoods that depend on them (Schindler *et al.*, 2010).

Due to opened movement routes, individual fish used alternative migration routes and additional habitats (I–IV). The effect of open migration routes for fish population is generally positive (I–IV), but potentially also negative in specific occasions (e.g. turbine channels, II). In waterbody segments with technical installations, biological fish features (e.g. body size, spatial and temporal preferences for movements, swimming ability, etc.) should be well considered as this may lead to significant improvement of the fish population state.

Table 1. Proportion of time (%) spent in different waterbodies and river sections during the study by individual asp tagged with acoustic transmitters. Only fish detected during > 1 year are presented. The largest value of habitat use for each fish is highlighted with grey background colour. Table modified from **III**.

Fish ID	Released	Detected (days)	Fish habitat usage (%)							
			L. Peipsi	Lower third of R. Emajõgi	Middle third of R. Emajõgi	Upper third of R. Emajõgi	L. Võrtsjärv	R. Pedja lower course	R. Põltsamaa and other tributaries	Oxbow lakes, gravel pit
714	03.04.12	746	–	–	26	43.1	6.1	24.2	0.7	–
806	10.11.11	736	11.7	4.8	44.9	38.6	–	–	–	–
715	03.04.12	640	27.9	0.5	34	36.8	<0.1	0.4	0.3	–
719	10.04.12	746	30.9	0.5	0.9	32.4	19.7	11.5	4	–
818	26.04.12	519	–	–	19.7	29.8	50.5	–	–	–
841	12.10.11	765	15.9	10.9	25.9	29.1	0.2	17.1	0.9	–
710	03.04.12	747	10	0.6	39.8	27.8	21.9	–	–	–
817	26.04.12	713	–	–	73.6	26	–	–	–	0.4
723	11.04.12	741	17.1	1.1	56.7	24.4	–	0.8	–	–
711	03.04.12	678	19.5	5.6	31.3	22.8	<0.1	19.5	1.3	–
822	28.04.12	754	9	7.6	52.8	22.3	<0.1	4.7	3.6	–
724	13.04.12	742	17.6	1.7	6.2	20.6	8.7	38.3	7	–
810	13.12.11	752	30.1	4.7	43.6	20.2	–	–	1.4	–
718	10.04.12	383	20.8	0.5	49.5	19.9	9.3	–	–	–
853	07.11.11	727	<0.1	29	49.3	19	–	–	2.5	–
846	17.10.11	759	18	0.5	40.7	17.2	–	22.4	1.2	–
725	13.04.12	522	–	–	–	15.2	42.9	29.4	12.4	–
815	24.04.12	707	19.9	0.4	59.5	14.1	–	3.8	1	1.2
844	15.10.11	761	–	40	41.7	13.6	4.8	–	–	–
808	25.11.11	763	16.4	1.3	70.7	11.7	–	–	–	–
852	02.11.11	743	6	32.4	50.5	9.6	–	0.7	<0.1	0.8
820	27.04.12	724	13.8	0.5	78	6	–	–	–	1.7
728	16.04.12	392	29.3	53	9	4.1	–	3.7	0.1	0.6

4.2 Fish Mortality and injury during downstream migration at the power station with multiple migration routes

4.2.1 Effectiveness of bar racks

To prevent downstream migrating fish from entering the turbines, a bar rack with 25 mm vertical openings (required by Estonian norms during the study) was present at the entrance of the turbine channel. Still, 21/24% of smolts descended through the turbines (103/6 individuals; fin-clipped or acoustically tagged smolts, respectively (**II**; Fig. 3). Smolts descended through the bar racks to the turbine at night. Some fish visited the turbine-channel several times, and two fish moved back from the turbine inflow channel to the reservoir during the day. Bar spacing of 25 mm did not fully prevent smolts from passing the rack (**II**). In another North Estonian river (Loobu) 0.01% of Atlantic salmon smolts were not physically able to pass through racks with 25 mm bar spacing (Anon., 2017). Bar spacing 10 and 15 mm seems to prevent the passage of most salmon smolts (Havn *et al.*, 2017; Thorstad *et al.*, 2017), and 25 mm bar spacing hinder only salmon smolts > 250 mm body length (Adam *et al.*, 2005; Larinier & Travade, 2002). Hence, only a few or even none of the largest smolts in our study may have been physically prevented by the 25 mm bar rack (**II**).

Bar rack openings that are larger than the fish width, may act as a behavioural or visual barrier and still reduce the proportion of fish passing (Adam *et al.*, 2005). In study **II** visual effect of the bar racks was reduced or insignificant as smolts moved through them both at night and during the day. Since completing this study, either 12 mm bar racks or 15 mm net racks are required for special rivers important for salmon, trout and/or grayling in Estonia (RT, 2019).

4.2.2 Impact of Kaplan-type turbines

According to the fyke net catches and diving surveys, mortality occurred only among the salmon smolts that descended through the turbine. Thirty-three (30%) of the 109 salmon smolts were found dead immediately below the power station. In 29 cases, external physical injuries were detected (mostly missing body parts). No acute mortality was recorded for 330 fish passing through the fishway (**II**; Fig. 4).

In addition to acute mortality, delayed mortality among the smolts that descended through the turbine was detected. During four to eight days after descent, 5 of 67 smolts that appeared uninjured after passing the turbines were found dead. Delayed mortality was not detected among the 69 fish that had descended through the fishway and spillway. Considering both the acute and delayed mortality, the total turbine-induced mortality was 36% (Fig. 4). Additionally we checked if lethally injured smolts released in the turbine outflow can be detected by fyke

nets or diving surveys. Only 7 of the 32 dead smolts were later recorded, indicating that the total turbine-induced mortality was underestimated (II).

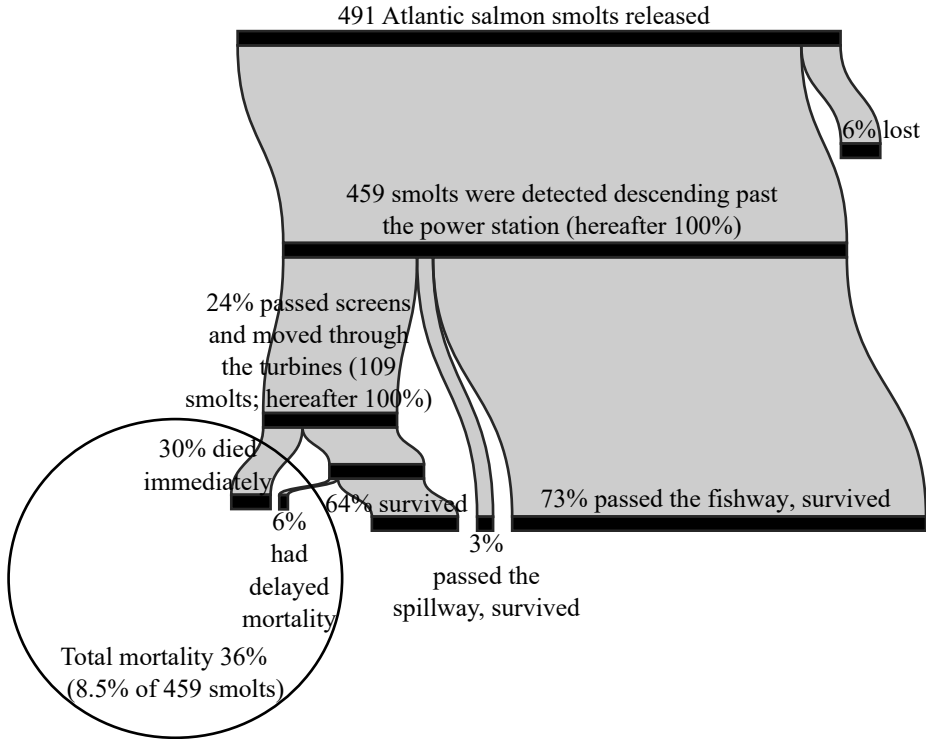


Figure 4. The use of different migration routes (fishway, spillway, turbine channel) by salmon smolts (acoustically tagged and fin-clipped together) and mortality rates of passing fish. The width of flows on this Sankey diagram are proportional to the smolts quantity.

Other studies report salmon mortality rate caused by Kaplan type turbines between 0–35% (Stier & Kynard, 1986; Larinier, 2001; Larinier, 2008; Gustafsson, 2010; Huusko *et al.*, 2012; Vikström *et al.*, 2020). Thus, the estimate for the mortality rate recorded in this study (36%) is one of the highest reported for Kaplan type turbines. There are several possible explanations for this. Local conditions facilitated direct observation of dead fish. A fyke net could be positioned in the fast-flowing turbine outflow channel where the injured or dead fish were carried with the swift flow, and it was also possible to detect dead fish on the bottom of the outflow channel by diving. In addition, Kaplan turbines were relatively small and fish had to pass closer to the harmful walls and blading (II). Such turbines generally have higher rotation speeds (Larinier, 2008), which could also elevate mortality rate in our study. Alternative methods (e.g. modelling) may cause underestimation of fish mortality (Vikström *et al.*, 2020). Mortality estimating that use direct observation of acute and delayed mortality are preferable.

Acute and delayed mortality recorded in this study must be regarded as minimum estimates. The acute mortality estimates may be underestimated as several predators, including American mink (*Neovison vison*) and goosanders (*Mergus merganser*), were present and able to remove dead or injured fish from the turbine tailrace (II). Some of the fish injuries may cause delayed mortality at a later stage, or injuries may reduce fish physiological adaptations to saltwater and thereby induce elevated mortality when they enter the sea (McCormick *et al.*, 2009; Zydlewski *et al.*, 2010). Stressed and disoriented fish may also be more vulnerable to predators after turbine passage (Larinier, 2001).

Most of the smolts used alternative migration routes (fishway, spillway) and the total mortality due to hydropower station on the R. Purtse was estimated at 8.5% (II; Fig. 4). Although screens may totally prevent smolts entering turbines, predation in the reservoir and physical injuries in bypass routes may still cause mortality for a large proportion of salmon smolts (e.g. 7–17% by each of these two factors in a study by Havn *et al.*, 2017).

Variation in fish behaviour, physiology, size, life history, etc. may lead to differences between species vulnerability to turbines. This may happen, e.g., due to the risk of rupturing the swim bladder (being lower for, e.g., salmonids and cyprinids but higher for, e.g., percids; Larinier, 2001) or differences in body size during the main downstream migration phase. The probability to physically pass screens is lower for larger individuals, but their collision probability with turbine blades is higher (Jacobson *et al.*, 2012).

4.3 Fish behaviour in relation to fish biological and habitat parameters

4.3.1 Relationship between fish size and sex with fish behaviour

Fish size. The probability that asp would descend from R. Emajõgi to L. Peipsi during a year correlated with fish TL (III). Most (94%) larger fish (TL > 70 cm) descended to L. Peipsi, while only 61% of the smaller fish did so. Such a migration pattern may have several reasons, e.g., nomadic or condition-dependent behaviour has been described for some cyprinid fishes (Brodersen *et al.*, 2008, 2019). Possible explanations for our results may involve an ontogenetic change in behaviour caused by the need for a larger home range or, alternatively, differences in feeding conditions between waterbodies. Hunting grounds for asp in L. Peipsi during the early summer seem to be good, due to higher water transparency (KESE, 2020; Wildlife Estonia, unpublished data) and a wider size spectrum of available fish prey.

The mean TL of smolts that descended through the turbine (187 mm) was smaller than the smolts that were released in the river (207 mm, II). Possibly, smolts could preferred the fishway (II), but smaller fish were less able to maneuver in the current and more often moved with the main flow through the turbines. There could also be a size selection by the bar rack in front of the

turbines (II), the largest smolts were possibly prevented or more reluctant to move through the rack with 25 mm bar spacing. Havn *et al.* (2017) similarly found that the probability of smolts choosing a fishway increased with fish TL and decreased with discharge.

Fish sex. Female vimba bream moved to sea earlier than males (I). The sexual differences in behaviour are consistent with differences in reproductive biology as fish males often spend more time close to spawning grounds than females (Lucas & Batley, 1996). Also, male vimba breams spend more time on rapids while females may stay downstream and visit spawning site only briefly (Lusk *et al.*, 2005).

Female asp entered the spawning tributary on average two days later than males (III); however, the difference was not significant (possibly due to low sample sizes). Fish remained in the spawning tributary on average for 12 days. During this period, both sexes performed relatively long (≥ 3 km) temporary movements back to slow flowing river sections. These sections were also used during pre-wintering, wintering and after the spawning periods (III). Deeper river stretches below rapids are necessary for both sexes, possibly for asp recovery between exhaustive efforts during spawning (Šmejkal *et al.*, 2017). Thus, conserving or restoring long-term availability of deep pools below rapids may be relevant.

4.3.2 Diel movement patterns of salmon smolt

The salmon smolts had a distinctive diel activity pattern descending past the hydropower station area. According to the diel dynamics of fyke net catches, 92% of the fish descended between 16:00 and 6:00. The stationary receivers in the fishway opening and in the reservoir registered movements towards and away from the fishway. The activity patterns based on these receivers resembled the diel activity recorded by the fyke nets, with the peak (92% of the movements) between 16:00 and 6:00 (II; Fig. 5).

Acoustically tagged smolts descended through the bar racks to the turbine at night, through the first bar rack between 22:06 and 02:22 and through the second (with 45 mm bar spacing, at the turbine intakes) about one hour later. Some fish entered the turbine-channel several times, and were also detected returning to the reservoir. These upstream movements were recorded only during daytime (II).

Data on smolt nocturnal activity were recorded between water temperature values 10–14 °C (II; EEA, 2020). In studies by Ibbotson *et al.* (2006) and Haraldstad *et al.* (2017), hourly rates of Atlantic salmon smolt migration did not differ or were higher during the day than at night when temperatures exceeded 12–13 °C. Smolt migration patterns and its changes can be explained as adaptations to predation avoidance (Haraldstad *et al.*, 2017).

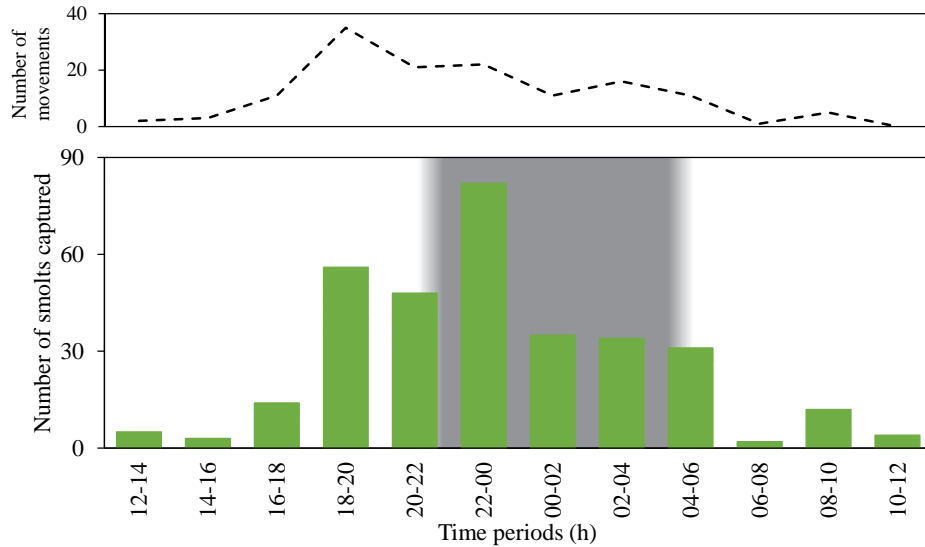


Figure 5. The diel distribution of fyke net catches during May 2015 given as a number of salmon smolts captured per 2-hour period (bars). Grey background indicates night. Dashed line indicates activity of acoustically tagged salmon smolts (14 May-7 June, UTC time + 3 h), based on movements between receivers deployed in the fishway entrance and reservoir. Figure modified from **II**.

Both fyke net catches and recordings of tagged fish indicated that the smolts were most active at night, starting ~4 hours before sunset and ending around sunrise. This indicates that operating turbines during the daytime and closing them at night could be an efficient mitigation measure (**II**). As daytime activity often increases towards the end of the season (Haraldstad *et al.*, 2017; Thorstad *et al.*, 2012), this is perhaps more efficient earlier than later in the smolt migration season.

Two methods to study fish activity gave similar results (Fig. 5). Still, the main peak in activity was slightly delayed for fyke-net catches compared with telemetry data. Fish avoidance of fyke-nets during the daytime (as one possible reason for this) should be studied further.

4.3.3 Correlation of fish movement speed with internal and external parameters

Asp movement speed was positively correlated with water temperature and discharge, but negatively with distance from L. Peipsi. Asp movement speed differed between upstream and downstream direction, the latter was faster. Fish movement speed also depended on the final movement target: fish were faster while moving between waterbodies than moving inside the same waterbody. No correlation was found between movement speed and temperature trend, discharge trend and fish TL (**IV**).

Asp movement activity was low for long periods when water temperature was near 0 °C. Segmented regression analysis showed that for downstream movement speed, a breakpoint was at 10.9 °C, with the highest mean near this temperature. For upstream movement speed, a breakpoint was detected at 11.3 °C, and mean speeds were the highest above this value. Fish movement activity was low for long periods when the discharge was low. Segmented regression analyses showed that for downstream movement speed, a breakpoint was detected at discharge of 110 m³ s⁻¹, with the highest mean speed close to this value. For upstream movement speed, a breakpoint was detected at discharge of 35 m³ s⁻¹, mean speed was the highest near this value (IV).

Fishes respond to temperature changes by altering behaviour and distribution (IV; Helfman *et al.*, 2009). For warm-water species such as asp, the relationship between activity and temperature was expected to be positively correlated. Segmented regression analysis revealed that this relationship is actually rather cryptic if studied by swimming direction. According to the linear mixed-effects model, movement speed was also positively correlated with discharge (IV). Discharge-related events may be important stimuli to initiate migration in asp as in many other fish, e.g. for salmonids (IV; Lucas & Baras, 2001). The rate of water discharge is associated with many factors, such as water temperature, turbidity, air pressure, cloud cover, pH and the concentration of many dissolved ions (Banks, 1969). Therefore, direct and indirect effects for fish behaviour are hard to distinguish.

During downstream movement, vimba bream passed faster the slow-flowing parts of the river than the rapids (I). The fastest speeds (up to 42.7 km day⁻¹) were measured in fish descending to the sea. Post-spawning asp moving towards L. Peipsi showed a similar trend (III, IV). The fastest upstream movement of vimba bream, 19.6 km day⁻¹, was achieved in autumn by the first fish that ascended from the sea to the wintering area. Downstream movement speed was on average 1.6 times greater than in fish moving upstream (I); the same trend was revealed for asp (IV). Variation in movement speed in vimba bream was higher than reported before (Erm *et al.*, 1970). This may be due to differences in methodology (telemetry vs external tags) or the size of study systems.

Asp swimming speed inside the same waterbody varied a lot depending on location. Asp maintained a high swimming speed in the lower third of the R. Emajõgi moving both upstream and downstream (III, IV). Vimba bream tended to behave similarly while moving downstream, but not upstream (I). The latter difference between asp and vimba bream could be due to a scarcity of suitable wintering areas upstream for vimba bream. Fish tend to be more mobile or less abundant in homogenous river stretches than in heterogeneous stretches. This pattern seems to be widespread and is possibly associated with greater variation in key microhabitats (Bruylants *et al.*, 1986; Lucas & Baras, 2001). High movement speed on the lower part of R. Emajõgi may therefore be caused by low number of oxbow lakes (providing food for asp) in this region and longer distances to spawning areas (III, IV).

Shifts in swimming speed (and direction) affect fish vulnerability to active and passive fishing gears. According to linear mixed-effects models (**IV**), high movement speed was usually related to large-scale habitat changes, which may indicate that making shifts in habitats may be time-critical for fish. As fyke-nets are usually directional, the vulnerability of fish also depends on swimming direction (Hladík & Kubečka, 2003; Hubert *et al.*, 2012).

Asp shifted towards the lake habitat during April and May, and to the tributary (spawning area) between July and November (**III**, **IV**). These fast movements contributed to the formation of temperature-dependent breakpoints for movement speed and direction close to a water temperature of 11 °C. Above this temperature, upstream movement speed increased suddenly and levelled off in a downstream direction (**IV**). Habitat shifts near water temperatures of 10 °C have also been described for other asp populations (Fredrich, 2003; Pfauserová *et al.*, 2019), when fish moved towards wintering habitats. Reducing the probability of incidental by-catch of non-target species (e.g. protected asp) is one major goal in modern fisheries management. Inversely, in the case of non-native fish (as asp may be, e.g. Merciai *et al.*, 2018; Pfauserová *et al.*, 2019), intentional overfishing is a common management technique by resource managers (Rytwinski *et al.*, 2019). Thus, fish location, swimming speed and direction data supported with relevant environmental variables (temperature, discharge) may be valuable for conservation and management purposes.

4.4 Annual and diel movement patterns of asp and vimba bream

4.4.1 Annual movement patterns and habitat use

Asp

General overview. Clear seasonal movement patterns were identified for asp (**III**, **IV**; Fig. 6) Asp alternated between habitats during the whole annual cycle (**III**). Overall, the riverine habitats were utilized more (mean 79% of time) than the lentic habitats. The usage of lentic habitats started shortly after spawning (late April or early May). During post-spawning and feeding periods, an average of 65% of the tagged fish descended to L. Peipsi (Fig. 7). After spending an average 71 days in the lake, they returned to R. Emajõgi and passed rapidly the lowermost third of the river. Fish leaving L. Peipsi mixed with the fish that had remained in the middle and upper section of R. Emajõgi, in the R. Pedja system and in L. Võrtsjärv. Thus, the fish were wintering mostly in the upper part of R. Emajõgi, close to the spawning areas. Asp movements towards the spawning areas before wintering (similarly to vimba bream, **I**) may be considered as an early phase of spawning migration (Kottelat & Freyhof, 2007) and may compensate for the rather short pre-spawning and spawning periods.

About one third of fish (generally the smaller ones; **III**) never descended to L. Peipsi during the post-spawning and feeding periods, or during the whole year. These fish mainly utilized R. Emajõgi and most of them visited L. Võrtsjärv during the summer.

The upper third of R. Emajõgi was the only section used by all asp that were tracked during a longer period than one year (**III**; Table 1). R. Emajõgi was also the only waterbody where tagged asp were detected throughout the entire study.

During the main feeding periods, fish entered the tributaries to a lesser extent than during the rest of the year. Some fish visited well-connected oxbow lakes after spawning in April and May. Smaller tributaries were visited by asp only during the post-spawning period (R. Ilmatsalu) or not at all (rivers Väike-Emajõgi, Laeva, Elva) (**III**; Fig. 6).

In our study the lakes were used for wintering to a lower degree than in other studies (Hladík & Kubečka, 2003; Pfauserová *et al.*, 2019). The use of lakes could be also underestimated in our analysis, as 20 fish that moved to lakes Peipsi or Võrtsjärv were never detected again. Also, 16 fish were lost in R. Emajõgi during our study, probably due to illegal catch, predation or tag malfunction.

Preliminary visiting of spawning tributaries by asp. Asp usually visited spawning sites or adjacent areas during autumn of the previous year (Fig. 6), but often moved away again and stayed for winter in other parts of the tributary, main river, or L. Võrtsjärv. The remaining fish visited tributaries only during the spawning period. Fish usually entered the tributary during high water discharge but when the water temperature was close to the mean entering temperature (7.4 °C), also during lower discharge (**III**).

Pre-spawning period. During or shortly after the ice broke up, at low water temperature (0.1–1.6 °C), and 3–20 days before the river discharge maximum, asp that had spent the winter in R. Emajõgi continued to move upstream or downstream, and some entered the tributaries. Asp covered 3–55 km during two weeks before the beginning of the spawning period, sometimes including up to 35 km long downstream migration (**III**).

Spawning period. During the spawning period, about half of the fish were recorded in R. Emajõgi, some in tributaries (rivers Pedja, Põltsamaa, Ahja and Tännasilma; Figures 1 and 6). Six fish had entered the lakes before the spawning time and probably spawned in non-monitored tributaries (**III**). Fish were not detected in the main historical spawning tributary, R. Väike-Emajõgi (**III**; Ristkok, 1974). The hydro-morphology of this river has been severely modified and it may not function as a spawning area for asp anymore. The spawning rivers and sections were similar between years, indicating the importance of the availability and protection of these key habitats. In complex systems, identifying possible weak subpopulations and focusing on their recovery should be a priority (**III**).

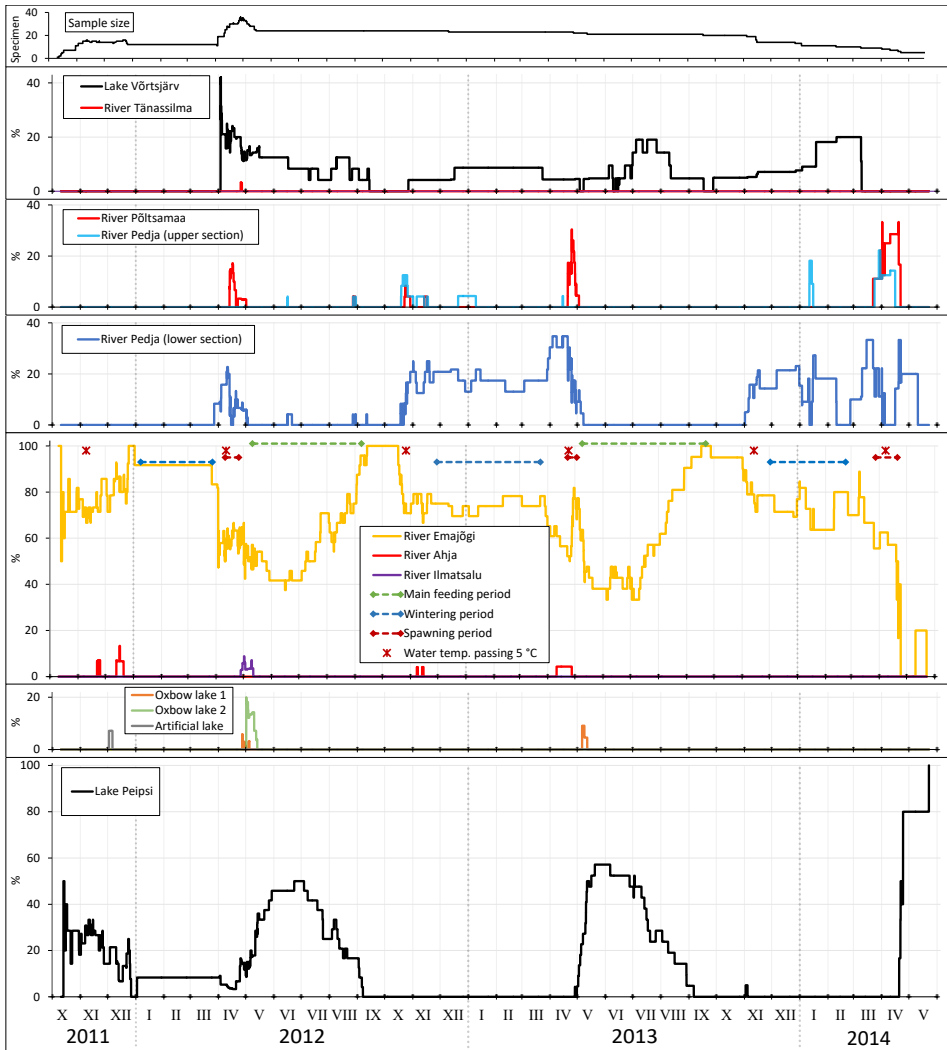


Figure 6. Habitat use of asp during autumn 2011– spring 2014. Continuous lines indicate the proportion of acoustically tagged asp in different waterbodies and sample size (upper panel). Figure modified from III.

Water parameters in tributaries during spawning. Asp usually entered the spawning tributaries during spring (average date 10 April and water temperature 4.0 °C). Asp always entered the tributary after the beginning of the largest spring flood. Some fish, after moving a long distance or coming from a lake, reached the spawning areas under rather low or high temperature. After experiencing a maximum water temperature of 4.4–10.9 °C (mean 6.9 °C), fish left the spawning tributary (III). This corresponds to earlier data on asp spawning temperature at 4–14 °C (Popova, 2002; overview by Riehl *et al.*, 2002). In R. Emajõgi, asp were positioned mainly near the few river sections with rapids during the spawning

time (between 34–62 km from L. Peipsi). Some fish also stayed in the main river near the tributary inflows up- or downstream from these rapids. Asp detected in R. Põltsamaa during the spawning period were located mainly in the lowest 3 km of the river.

Post-spawning period. In between leaving the spawning areas and period with optimal temperature for feeding, the fish showed a multitude of behaviours. Most fish descended towards L. Peipsi, some reached L. Võrtsjärv or moved towards it. Some asp stopped one or several times during the post-spawning movement phase. In the Põltsamaa-Pedja system, 44% of the fish remained near their spawning areas, a few kilometres downstream from the confluence area, for 1–13 days after leaving the spawning site. Most fish stopped or reduced their movements in R. Emajõgi, some visited tributaries. In early May, up to 20% of the fish were located in well oxygenated oxbow lakes. This rate was possibly underestimated as few oxbow lakes were monitored (III). Cyprinids may need recovery areas in slow-flowing waters during the post-spawning period (Clough *et al.*, 1998).

Main feeding period. During this period, the fish were located mainly in R. Emajõgi and L. Peipsi (Fig. 6). Some fish also stayed in L. Võrtsjärv or tributaries but not in oxbow lakes. The median date for entering L. Peipsi varied from 24 April 2014 to 14 May 2012 (Fig. 7). The median date for returning to R. Emajõgi was 25 July 2012 and 16 July 2013, and migration was completed by mid-September. The upper part of R. Emajõgi was used extensively as a feeding habitat (III). Leaving a lentic waterbody during the early feeding period appears to be uncommon for asp (Fredrich, 2003; Hladík & Kubečka, 2003; Horký & Slavík, 2017; Pfauserová *et al.*, 2019). Most similarly, the semi-migratory asp in Caspian Sea basin started to ascend the river during October (Kottelat & Freyhof, 2007). Descending and the early return may be related to the change in the optimal feeding habitat or the availability of prey. The leaving time of L. Peipsi coincides with the warmest period of the year (July-August), when cyanobacterial blooms are common; blooms may result in fish kills (Kangur *et al.*, 2005). Fish leaving cyanobacterial bloom areas has been reported in Poland (Wojtalik *et al.*, 2006).

Asp concentration in the meandering part of R. Emajõgi during the main feeding period may also be the result of good hunting conditions (III). Oxbow lakes are important spawning and nursery areas for several fish species, and potential prey for asp may move from them to the main river during spring and summer (Borcherding *et al.*, 2002; Hohausova *et al.*, 2003; Lucas & Baras, 2001). These movements may be particularly extensive during summer hypoxia in oxbow lakes (Ristkok, 1969; Wildlife Estonia, unpublished data).

Pre-wintering and wintering periods. After the main feeding period, all tagged fish stayed in R. Emajõgi for about 2–6 weeks (Fig. 6). Afterwards, part of the fish moved to the tributaries; some fish moved to the lakes for wintering (III).

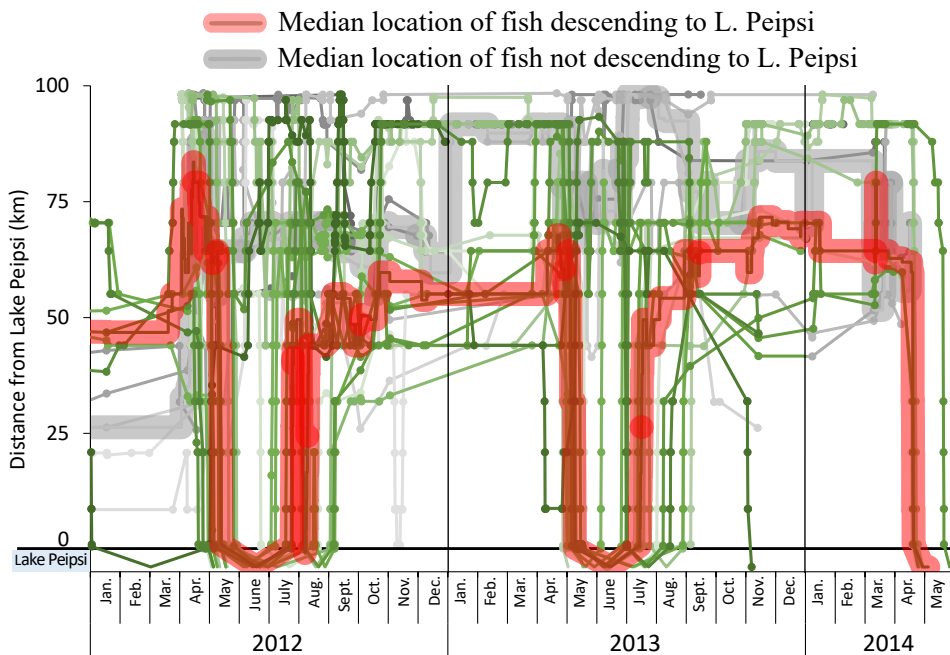


Figure 7. Riverine migration of asp between R. Emajõgi and L. Peipsi. Dots with thin lines indicate locations of individuals, colours represent fish behaviour type (green: descending, grey: not descending to L. Peipsi during one calendar year). Red and grey thick lines show the median location of fish with different behaviour types. Figure modified from **III**.

The majority of the fish (80–96%) wintered in rivers, mainly in R. Emajõgi (Fig. 6). Most of the remaining fish were concentrated on the lower 4 km stretch of R. Pedja. Fish that spawned in tributaries moved more between waterbodies during winter than fish that remained and presumably spawned in the main river. Fish wintered near their subsequent spawning areas. The wintering locations in R. Emajõgi were different for individuals that subsequently spawned in rivers Põltsamaa and Pedja, and those spawning in R. Emajõgi (average 73 and 52 km from L. Peipsi, respectively) (**III**).

The preference by asp to spend the winter in rivers rather than in lakes (**III**) is interesting, because wintering in reservoirs, or even only spawning in rivers and spending the rest of the time in lacustrine environments is reported in other studies (e.g. Hladík & Kubečka, 2003; Pfauserová *et al.*, 2019). For larger rivers such as Terek and Ili, prewintering migration into rivers has been reported, whereas for highly modified or smaller rivers it may be absent (Mamcarz *et al.*, 2008). In the R. Elbe, part of the asp population may leave the main channel during wintering due to the lack of deeper and slower pools (Fredrich, 2003). In our study system, wintering in rivers is likely more optimal for asp as shallow lakes Peipsi and Võrtsjärv as well as oxbow lakes may be hypoxic during the winter (Järvalt *et al.*, 2004; Kangur *et al.*, 2013; Wildlife Estonia, unpublished).

Movement speed. Mean downstream movement speed reached its maximum in May (1.5 km h^{-1}), while mean upstream speed was highest in July (1.1 km h^{-1}). Minimum movement speeds ($< 0.5 \text{ km h}^{-1}$) were recorded in January and February. The maximum recorded speed for an individual fish moving downstream was 5.4 h^{-1} and upstream 2.7 km h^{-1} (IV). Reported maximum speeds are higher than recorded with similar methodology for other cyprinids (e.g. vimba bream, I). Such sustained swimming speeds (or other estimates) are rarely measured in natural conditions (Beamish, 1978; Peake *et al.*, 1997), but may be more relevant to address practical questions. Although asp seem to have a good swimming ability, they also tend to avoid rapidly flowing waters, including both ordinary and modern fish passes (Fredrich, 2003; Horký & Slavík, 2017). Slow flowing fish passes with higher discharge may be required for asp if removing or not constructing a migration obstacle is not possible.

Fish movement distance and home range. Cumulative fish movement distance during one month correlated with fish home range size. Fish moved an average distance that was 1.3 times longer than its home range size within one month. After spawning in April and May, when fish performed long one-directional movements towards feeding areas, the difference between home range size and distance travelled was small, close to 1:1. In June and July this difference was relatively large, indicating high activity inside the home range. According to home range size as well as distance travelled, fish were most active during April-September and least active during October-March (mean monthly home range for all fish 18–45 km and 2–12 km, respectively) (IV). In southern areas differences in home range size among seasons varied less (Horký & Slavík, 2017).

The average annual cumulative movement distance covered by individual asp was about 350 km (maximum 522 km). About 78% of the distance was passed during the relatively short period (~40% of the year) with water temperature $> 12 \text{ }^{\circ}\text{C}$. The period with temperature $> 15 \text{ }^{\circ}\text{C}$ lasted about one third of the year, during which most (up to $\frac{3}{4}$) of the distance was passed. Asp activity measured as mean movement speed decreased by 68–78% in 2012 and 80–82% in 2013 during the period of the year that was not optimal for feeding (IV). This is more than measured for the warmest and coldest season in the southern part of asp distribution area (Horký & Slavík, 2017). Asp is considered a warm-water species (Krpó-Ćetković *et al.*, 2010; Mikelsaar, 1984) and has been shown to cease feeding when water temperatures fall below $12\text{--}15 \text{ }^{\circ}\text{C}$ (Mikelsaar, 1984; Trzebiatowski & Leszczewicz, 1976), with a declining condition factor indicating a negative energy balance during winter (Krpó-Ćetković *et al.*, 2010). In Serbia and Poland, most asp had empty guts between September and March, and all ceased feeding during February (Trzebiatowski & Leszczewicz, 1976; Krpó-Ćetković *et al.*, 2010). In Estonia near the northern border of the distribution area of asp, the duration of periods with warm water temperatures and of sufficient daylight may be a limiting factor for a warm-water species. At high latitudes and altitudes, the cold period is often considered critical for fish populations, and various behavioural adaptations may help to buffer the energy deficit (Heggnes *et al.*, 1993). Fish species with higher preferred temperatures may tolerate cold

conditions, but are not able to actively utilise resources (Shuter *et al.*, 2012). Maximising activity during the short, favourable period in order to achieve a positive overall energy balance may be a prerequisite for fish to survive in the cooler margins of their distribution area. However, high activity of asp over a restricted time period (**IV**) may increase their vulnerability to risk factors such as passive fishing gears and facilities abstracting water (e.g. for turbines). Migration delays may further shorten an already short feeding period, and affect the long term survival, especially in northern asp populations. On the other hand, predicted climate warming may increase the length of the optimal time for feeding in terms of temperature, light as the periods with ice cover will shorten (Ficke *et al.*, 2007; Lehtonen, 1996).

All fish in our study had an annual home range longer than 40 km (**IV**). In the much larger R. Elbe, most asp (tracked for at least one year) had a yearly home range size of only 1–40 km (Fredrich, 2003). Neither Elbe nor Emajõgi rivers had obstacles for fish migration. This seems to contradict the idea that fish home ranges increase with the size of the waterbody (Woolnough *et al.*, 2009). However, it is in line with the larger home range predicted for terrestrial animals at higher latitudes (Harestad & Bunnell, 1979). Large scale habitat structures, such as the distance between spawning, feeding and wintering areas, are probably the main determinants for asp home range size. According to monthly home range size, asp in R. Emajõgi were most active during the spring and summer months (**IV**). This differs from studies on asp annual activity at lower latitudes (49–53 °N). Based on home range size, Pfauserová *et al.* (2019) found that activity was low outside the spawning period (March–April). Horký and Slavík (2017) described low asp activity during spring and winter based on home range size and diel movements.

Mean yearly home range of asp was ~80 km. Maximum daily home range (47 km) was in line with calculations made by Fredrich (2003), who estimated daily home range up to ~50–60 km. Home range estimates are used for decision-support in conservation biology (Fauvelle *et al.*, 2017). This metric is important, but gives insufficient information on the actual activity of fish inside its home range, which is crucial information for estimating fish vulnerability to various risk factors (e.g. vulnerability to fishing gear, turbines/water intakes, migration obstacles, etc). The actual asp activity varied individually and was 1–7 times their home range size. Of all activity events, 74% were short non-directed movements periodically detected by a single receiver. Two thirds of longer movements (between two or more receivers) were habitat shifts between waterbodies. Our results indicate that relatively small home range size of asp may be a result of low movement activity, and/or a high proportion of local movements (**IV**). High activity inside a restricted home range may render the fish vulnerable to passive fishing gears, as well as turbines, water intakes etc. For mitigation purposes, this knowledge could be supplemented with information on diel activity patterns. For example, stopping or reducing hydropower operations during the short twilight periods when fish are active might be a substantial contribution to improve the efficiency of fish pass systems (Lucas & Baras, 2001).

Vimba bream

Vimba bream alternated between habitats during the annual cycle. *Vimba bream* used riverine waterbodies (rivers Pärnu and Navesti) during 62% of the year. Brackish habitats (sea) were used after spawning (first half of June) (I; Fig. 8).

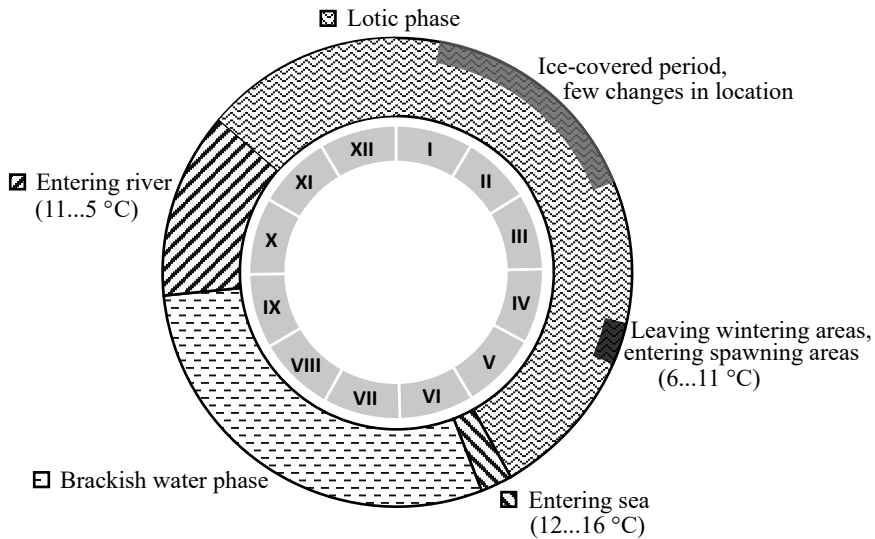
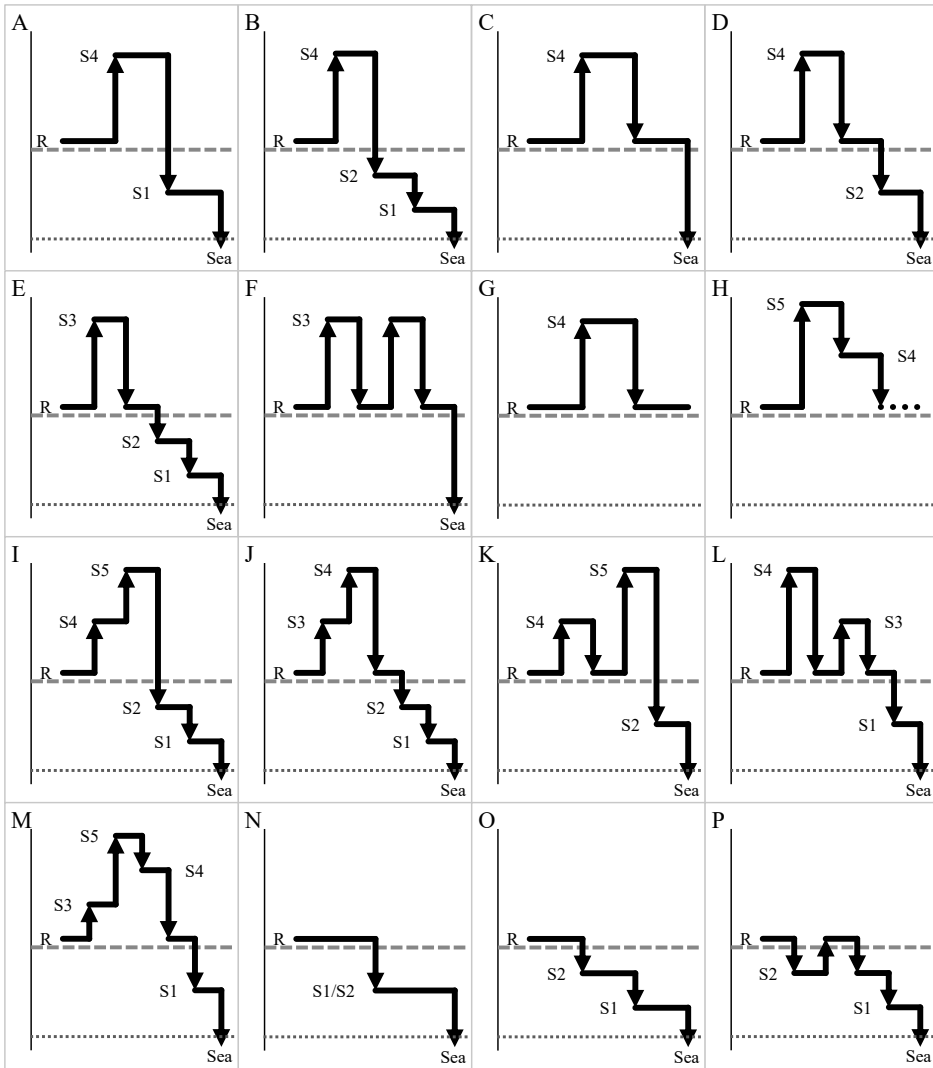


Figure 8. Habitat use and timing of migrations of vimba bream during a year (spring 2013–spring 2014).

Spawning, post-spawning and feeding periods. Soon after tagging and release on 15 May 2013, the fish started moving and the first fish left the reservoir during the first night and the last fish on 8 June. The fish moved upstream ($N = 15$) and downstream ($N = 13$) from the reservoir. Two fish stayed in the reservoir until their transmitters were not detected anymore. Two individuals, which were the first to leave the reservoir, made the longest (25 km) upstream migration. Most of the fish moved to spawning areas situated between 13 km upstream and 7 km downstream from the release site. Two fish descended to the sea without stopping in any spawning areas. The maximum number of fish in the spawning areas was registered by late May (I; Fig. 2).

Descending of fish from upstream spawning grounds and passing the dam was first observed on 21 May and was completed on 3 June (Fig. 2). By that time, the first fish had reached the sea. By 8 June, eight individuals remained in the lowermost spawning area below the dam. Migration to the sea was completed on 13 June (Fig. 8). However, one male remained in the reservoir for more than one year and descended to sea only after the spawning period in 2014 (I).

The riverine movement patterns of 24 individuals that migrated to spawning areas were variable and could be divided into 16 different types (Fig. 9). Thirteen fish were detected in more than one spawning area.



Movement sequence

Figure 9. Graphic illustration of habitat use sequence of vimba bream individuals during the spawning period. Grey dotted line indicates the sea, dashed line Sindi dam, R the reservoir, S spawning areas (with sequence number), \uparrow upstream movement, \downarrow downstream movement, — staying within a spawning area or the reservoir, . . . the fish was lost. Vertical axes indicate sequences of movement direction and stops on the lowermost 29 km of the river, whereas horizontal axes indicate the movement sequence during the time period 15 May 2013–16 June 2013. Time and space are not to scale. Figure modified from I.

Nine fish remained for a while in the reservoir, both between movements to different spawning areas, and before moving to the sea. Fish that moved upstream from the reservoir stayed in up to three different spawning areas before moving back downstream. When descending to sea, some fish moved directly and others stopped in one or two downstream spawning areas. Eleven fish moved to downstream spawning areas after release and then to the sea. This may indicate that fish could lose the stimulus for upstream migration after being stopped by the dam or in the reservoir. One fish that moved to a downstream spawning area later passed the dam and returned upstream into the reservoir. This unique movement pattern was repeated by the same individual during the next spawning season (I).

Our study design did not reveal the full complexity and individual variation of vimba bream behaviour. More transmitters and receivers are needed to study the movement pattern on a finer scale. For example, detailed information on mobility inside and between spawning areas may be useful for restoration of vimba bream populations in rivers (I).

Pre-wintering, wintering and pre-spawning period. Eight of 20 vimba bream that descended to the sea remained there for 115–159 days and returned to the R. Pärnu for overwintering (Fig. 8). Two individuals remained in the river mouth area, and ten fish were not detected again. The first fish returned to the river in late September, while the main migration occurred in October–November (between water temperature values 5–11 °C). The four fastest fish migrated to the wintering area (about 9–11 km from the river mouth) in 8–26 hours, while the slowest fish spent two months to cover this distance (I). Autumn migration may be longer (Calles & Greenberg, 2007) and take place at higher temperatures (Žiliukas & Žiliukienė, 2002). All vimba breams had reached the wintering area by mid-January when ice cover formed. Some fish probably remained in the brackish water for winter (I). Migration of vimba bream to freshwater occurs in both autumn and spring (Erm *et al.*, 1970; Volskis *et al.*, 1970). Wintering in brackish water may be related to poor wintering conditions in the river. In favourable conditions vimba bream is also able to winter in other habitats (e.g. nature-like fishway, Calles & Greenberg, 2007). Most sea trout and anadromous Arctic char *Salvelinus alpinus* in northern areas stay in freshwater during winter if conditions are good, otherwise they may stay at sea (Jensen & Rikardsen, 2012).

The vimba breams that entered the river in autumn, spent 152–203 days (mean 174 days) before initiating upstream movement in spring. Vimba breams also performed movements in the wintering area. They were least active under the ice cover from early January until early March, before migration to the upper part of the wintering area. Fish later changed their location frequently, usually within one day. After ice-break in the second half of March, the water temperature increased from 1.0 to 4.0 °C, the water discharge tripled, and all eight fish moved downstream. Then water level receded and temperature increased from 5.8 to 11.4 °C in mid–April and all the fish moved to the spawning areas below the dam (Fig. 8). Two of the vimba bream also passed the dam and moved further upstream (I). Very high discharge may inhibit fish upstream migration (Lucas & Baras, 2001) and can possibly also flush down fish (I).

The short river section below the first rapid was intensively used during the winter period and also in spring when fish became active (**I**). The high concentration of fish and their mobility make the fish potentially vulnerable to passive fishing gear. This should be considered when designing management and protection rules for vimba bream.

4.4.2 Diel movement patterns

Asp

General diel activity. Asp activity was related to varying light availability during the diel cycle (Fig. 10). Activity levels were higher during dawn and dusk than during the day and at night for most of the year (**IV**). At high latitudes, under natural photoperiods and temperatures, some nocturnal species become diurnal during the short days of winter (Reebs, 2002). Our data show that crepuscular species such as asp may also become diurnal during the short winter days in the northern part of the distribution range.

Asp in our study area had activity peaks during the diel cycle within all seasons, including spring and winter (**IV**; Fig. 10), which to our knowledge has not been shown before. Contrary to our results, asp in the R. Elbe were more active during the day and twilight in summer and only during the day in autumn (Horký & Slavík, 2017); the reasons for this difference remain unknown. The movements of small fish, optimal prey for asp, between the main river and lateral waterbodies (Trzebiatowski & Leszczewicz, 1976; Vašek *et al.*, 2018) may be restricted to the twilight period (Borcherding *et al.*, 2002). Thus, the asp diel activity patterns could be explained by a combination of prey availability and sufficient light for efficient hunting. However, the presence of clear diel rhythms with higher activity during light hours also outside the feeding season may indicate the presence of other factors in addition to prey availability. Foraging success and predation risk are commonly driving forces to develop diel activity rhythms (Reebs, 2002). Predation seems to be less relevant for asp during the cold season. In general, there is a lack of literature on the overwintering behaviour for piscivorous species, especially cyprinids, in rivers (Jurajda *et al.*, 2018).

The activity during dawn was higher than during the rest of the diel cycle during most of the year, whereas higher activity during dusk was not observed in late summer and early autumn (July-September) (**IV**; Fig. 10). According to a sport fisheries study in Finland (Lehtola *et al.*, 2006), asp feeding activity as indicated by a willingness to bite on fishing gear showed a similar trend. The willingness to bite was high during mornings and evenings in the late spring and summer, but from August only in the mornings.

Variation of daily activity levels has a bearing on the design of regulations and sampling of fish communities which include asp, e.g. when applying the European standard EN 14757:2015 for fish sampling. A longer (24 hour) sampling period may sometimes be necessary to achieve comparable results when investigating spatial/regional and temporal differences in species abundance (**IV**).

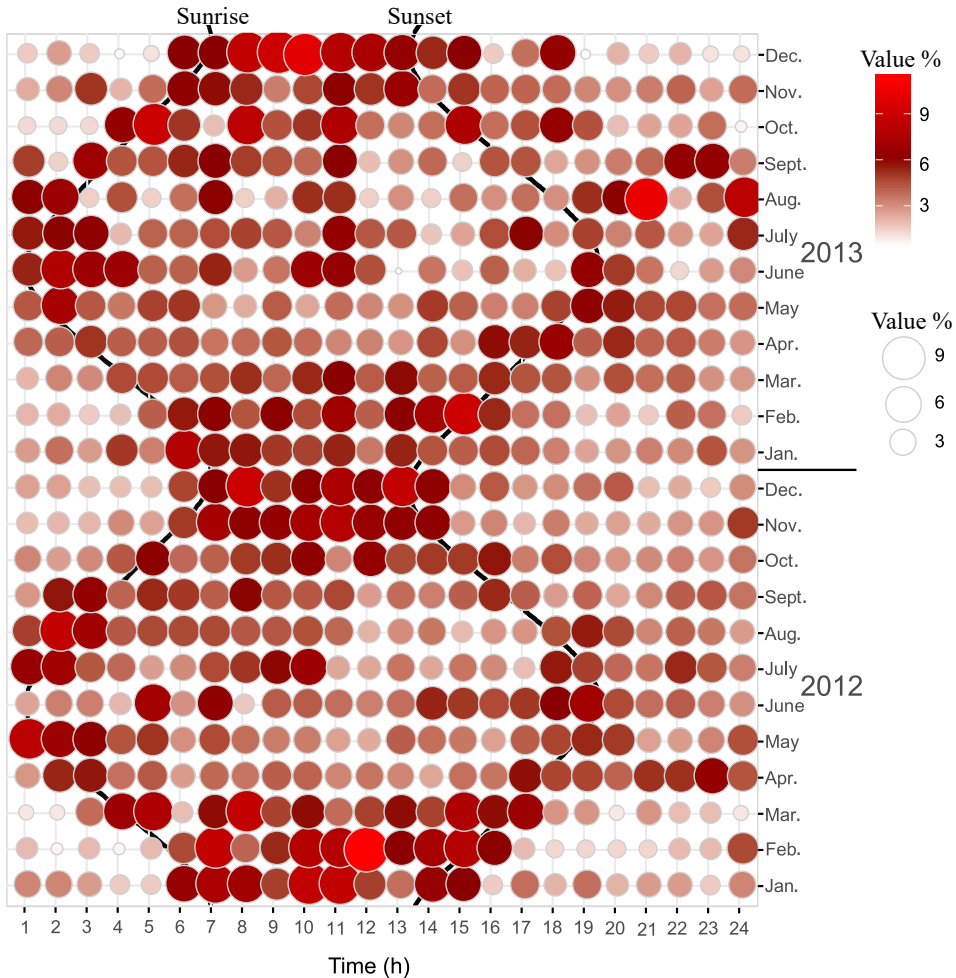


Figure 10. Diel movement activity of tagged asp during 2012 and 2013. Red dots indicate the proportion of activity events per hour during each month (full hour \pm 0.5 hrs). Black lines behind the data indicate the time (UTC) of sunrise and sunset. Figure modified from **IV**.

Asp annual and diel activity patterns (**IV**; Fig. 10) as well as habitat use and migration patterns were rather similar between the years (**III**; Fig. 6). Similar behaviour has been shown for asp elsewhere: strong spawning site fidelity (Pfauserová *et al.*, 2019), repetitive seasonal protandry (Šmejkal *et al.*, 2017), and diel spawning activity dynamics (Šmejkal *et al.*, 2018). This indicates that for any individual asp population, conservation management plans can be based on knowledge of the behaviour of fish in relation to simple predictive factors such as date of the year and time of day. According to our linear mixed-effect model, these predictive factors can be supported with environmental variables such as water temperature, discharge, and waterbody segment inside the fish's home range.

Direction of movement related to time of the day. There were differences in downstream and upstream movement activity levels between dawn and the rest

of the diel cycle, day and the rest of the diel cycle, and night and the rest of the diel cycle (all months pooled). There were no such differences between dusk and the rest of the diel cycle. Thus, during the entire study period, fish moved more actively upstream during dawn and the day, and more actively downstream at night. Risk ratios for upstream movements were 1.14 and 1.25 for dawn and day and for downstream movements 1.08 and 1.25 for dusk and night (all months pooled, **IV**).

In specific months, asp performed upstream movements 1.3–2.2 times more intensively than downstream movements during dawn and day, and downstream movements 1.2–1.8 times more intensively during evening and night (see risk ratios in Table 2).

Table 2. Directed movement activity levels of tagged asp during four diel phases of each month, pooled for all study years. RR represents the risk ratio to swim upstream or downstream during a diel period compared to the rest of the day. Symbol “↑” indicates fish moving relatively more actively upstream than downstream, “↓” moving relatively more actively downstream than upstream, and “NS” non-significant differences. Table modified from **IV**.

Month	Day phase			
	Dawn	Day	Dusk	Night
Dec.	NS	NS	NS	NS
Nov.	NS	NS	NS	NS
Oct.	↑, RR = 1.5	NS	NS	NS
Sept.	NS	NS	NS	NS
Aug.	↑, RR = 1.4	NS	NS	NS
July	NS	NS	NS	NS
June	NS	↑, RR = 1.4	↓, RR = 1.8	NS
May	NS	↑, RR = 2.2	↓, RR = 1.2	↓, RR = 1.2
Apr.	NS	↑, RR = 1.8	NS	↓, RR = 1.4
Mar.	NS	↑, RR = 1.3	NS	NS
Feb.	NS	NS	NS	NS
Jan.	NS	NS	NS	NS

Fish swimming direction differed between diel periods during six months of the year (March–June, August and October) (**IV**; Table 2). Our observations of asp upstream and downstream movement activity at night, contradict the assumption that asp may interrupt migration in darkness (Fredrich, 2003). During the spawning period, asp activity may be cyclical during the 24-hour period due to periodic gathering in spawning areas (Šmejkal *et al.*, 2018), but this is not relevant for the summer and autumn months. Downstream movement may also be a result of increased passivity by the fish or increased river discharge, and subsequent upstream movement during the morning or day is compensatory. In contrast, vimba bream moved upstream at night (**I**). Roach (*Rutilus rutilus* L.) may seek areas with slower water current at night (Hammer *et al.*, 1994). This may indicate that any diel cycle in the movement direction mainly depends on the location of the most optimal habitats for feeding, spawning and resting (refuge).

Vimba bream

General diel activity. There was a significant diel variation in activity in spring, autumn and winter but not in summer. The fish had the highest activity levels (per time unit) at dawn or dusk during the entire study period. The fish were generally least active at night (Fig. 5 in I).

Direction of movement related to time of the day. Between ice break and spawning, vimba bream was the most active during dawn, then during dusk. From 20 March to 19 April, most of the upstream movement occurred at 16:00–17:00 hours (UTC) and most of the downstream movement at 03:00–04:00 hours (Fig. 11). The sunrise during this period was between 2:59 and 4:24, sunset between 16:36 and 17:44. Similar diel rhythm in movement direction was also at the end of the spawning season. This pattern may be associated with feeding, or searching for suitable spawning sites (I).

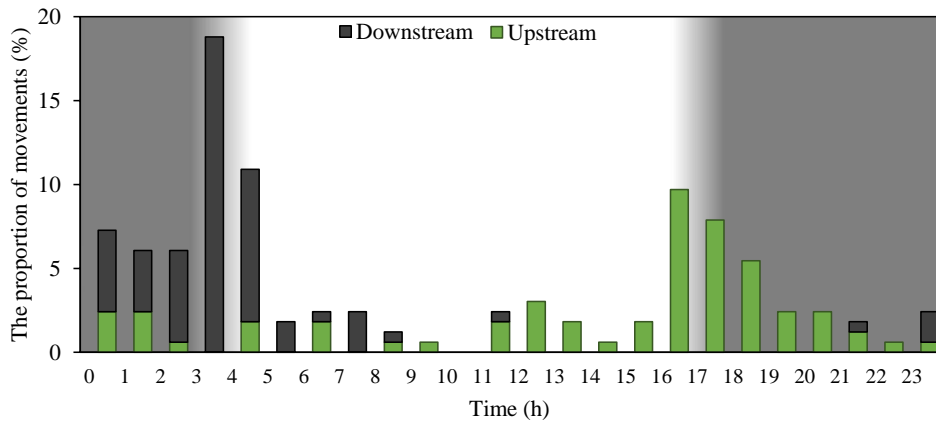


Figure 11. Diel activity of upstream and downstream movements of vimba bream before the spawning period (20 March–19 April) in 2014 (UTC time), based on receiver detections downstream from the lowermost spawning area. Grey background indicates period from sunset till sunrise. Figure modified from I.

In general, the vimba bream were more active during twilight than at other times of the day (I). Diel activity patterns for vimba bream in rivers during all seasons, to the best of the authors' knowledge, has not been presented in literature before. A higher mobility rate with location shifts during twilight has also been described for several other cyprinids, e.g. dace (*Leuciscus leuciscus*), chub (*Squalius cephalus*) and roach (Clough & Ladle, 1997; Baade & Fredrich, 1998; Fredrich *et al.*, 2003). Also, several non-cyprinid fishes, e.g. Atlantic salmon and pike-perch *Sander lucioperca*, show clear diel variation in their behavioural patterns (Lilja *et al.*, 2003; Davidsen *et al.*, 2008; Horký *et al.*, 2008). This pattern may be a compromise between diurnal predator avoidance, the advantage of using vision when moving and feeding, and feeding efficiency connected to the diel variation in the behaviour of the prey.

5. CONCLUSIONS

This study concentrated on the investigation of movement patterns of the migratory lithophilous fish species in a riverine environment with open or disrupted movement conditions. Objectives of this study stated in paragraph 2 were achieved as summarised below.

Our study revealed the great importance of open and safe migration routes for lithophilous migratory fish, especially if important habitats (e.g. spawning grounds) are limited. Half of the vimba breams caught downstream and released in the reservoir of the power plant continued their upstream migration to historic spawning grounds. Most salmon smolts descending to the sea preferred natural type fishway over the turbine channel. The mortality of smolts descending through Kaplan-type turbines was very high and racks with 25-mm bar spacing were ineffective in preventing smolts from entering turbines. Descending was nocturnal, which possibly lowers the visual effect of the racks. Cyprinids vimba bream and asp with access to diverse habitats had complex movement patterns. Patterns differed between individuals and resulted in diverse (but for asp inter-annually similar) habitat use. Populations used several waterbodies and its sections for spawning, asp also for feeding, wintering and post-spawning recovery.

Behavior of the studied species was somewhat predictable depending on both fish biological (size, sex) and habitat parameters (water temperature and discharge, river section, movement direction and target). Downstream migration speed of vimba bream was higher in slow-flowing river sections than in rapids; females reached the sea earlier than males. Downstream migration speed was higher than upstream for both vimba bream and asp. Asp moved faster between waterbodies than within a waterbody, fish speed was high also close to L. Peipsi. Asp speed was positively correlated with water temperature and discharge, but the relationship was never linear.

Vimba bream and asp had distinctive diel and annual movement patterns. A remarkable proportion of asps migrated to lakes after spawning in tributaries but returned to the lake in late summer. Asp tended to visit spawning tributaries during previous autumn and wintered near spawning areas. Vimba bream descended to the sea soon after spawning and returned to the river during autumn for wintering. Vimba bream performed considerable movements while in the wintering area, especially after ice-break. Activity during twilight was characteristic for both cyprinids. For asp it was supplemented with daytime activity during short winter days; dusk activity disappeared after midsummer for some months. Asp performed upstream movements more intensively than downstream movements during dawn and the day, and downstream movements more intensively during the evening and at night; during twilight vimba bream behaved contrary.

SUMMARY

We investigated movement patterns and habitat use of adult migratory cyprinids asp and vimba bream and Atlantic salmon smolts in their vulnerable riverine environment. Acoustic telemetry was used as the main method.

Access of migratory freshwater fish to remote limited spawning areas is critical for population survival. The requirements for home range size and diversity in behaviour of such populations may be larger than generally described, particularly for asp. The number of natural migration routes between essential habitats may be strictly limited (e.g. one river stretch) and may pose continuous and unexpectedly high harm (e.g. turbine channels) despite applying all required protection measures. If migration routes are obstructed by any migration barrier, fish natural habitat use may potentially become restricted during all seasons. As a result, the population can be negatively affected or even become extinct. This can happen unexpectedly as some essential habitats may be unknown or have changed. Restoring of spawning areas and/or routes to spawning grounds may be effective already short-term. The best option for fish is restoration of natural hydromorphological conditions (removal of the migration obstacle). Near natural solutions, even with relatively small discharge, may also provide good alternatives, at least for downstream movements of salmon smolt. Suitability for other species should be considered as well but they are especially relevant for native migratory species performing catadromous, anadromous or potamodromous movements. Moreover, all measures may benefit on knowledge of fish behaviour, which is related to various internal and external parameters (fish size, sex, illumination, water temperature, discharge, flow direction, river section, and targeted waterbody by fish).

Seasonal and diel migration patterns of asp and vimba bream were studied in detail. Both cyprinids started their migration towards spawning areas very early, during the previous autumn (vimba bream) or even midsummer (asp). Such an early return of asp to rivers from lentic areas was not known earlier. Wintering areas of asp and vimba bream in rivers were close to spawning areas, which enabled them to avoid long migrations during cool and short prespawning periods. This is potentially beneficial for thermophilic fish living in northern areas and resulted in a higher difference in activity during warm and cold periods than reported before. Most vimba bream visited more than one spawning area, which was possibly related to their batch-spawning behaviour. Asp spawned during unexpectedly low temperatures, which enabled earlier migration to feeding areas. During feeding periods asp utilised lakes and the main river near oxbow lakes, which probably provide food for piscivorous asp. Some and usually bigger asp descended to lakes for feeding but returned to the river relatively early, which coincided with the beginning of toxic algal bloom period, but it may also be related to a good hydro-morphological state of the target river stretch (Natura 2000 area). Fish home range size was unexpectedly high for asp (mean about 80 km and min 40 km for a year). In the lake-river system, asp actively moved

inside and between at least four Natura 2000 areas, as well as in the adjacent unprotected areas.

Significant variation in diel movement activity was detected during most (vimba bream) or all (asp) seasons. Diel activity patterns for vimba bream in rivers during all seasons, to the best of the authors' knowledge, has not been presented in literature before. According to previous knowledge of asp, continuous variation in diel activity during a year was unexpected. Diel activity patterns also differed among seasons and for asp also usually even among months. During all months, asp had activity peaks around sunrise and/or sunset; this tendency was generally characteristic for vimba bream as well. Asp became active during short daytime periods (October-March) but often remained passive during daytime for the rest of the year. In other words, asp crepuscular activity was replenished with diurnal activity during suboptimal times for feeding, and not during summer as described for the southern population. Elevated activity during dusk notably disappeared in late summer and early autumn as stated also in Finland. The variation in diel activity should be taken into consideration when applying the European standard EN 14757:2015 for sampling fish. With the variation in diel activity levels, a 24-hour sampling period may sometimes be necessary to achieve comparable results when investigating spatial/regional and temporal differences in species abundance.

Knowledge of seasonal and diurnal movement patterns of asp, as well as behavioural similarity between years, is essential while considering conservation, management and monitoring options in light of discussions to open fishery for asp. Another practical value of this study in direct demonstration of hydropower development dangers as well as usefulness of restoring river connectivity. Conservation activities are more successful if wider scientific knowledge is available. The results described in this thesis may help to analyse relevancy of conservation, management and monitoring programmes for other migratory fish species.

Most waterbodies and their catchments are in the focus of human activities, and will be even more in the near future. No single recipe can be given to keep fish fauna diverse and viable. For migratory fish, open and safe access to spawning, feeding and wintering areas is of utmost importance, especially if some habitats, e.g. spawning grounds for many lithophilous fish, are limited. This study highlighted the need to determine the most important habitats and most vulnerable phases of life for migratory fish species. For this, telemetry provides excellent opportunities and a high degree of trust in the results.

SUMMARY IN ESTONIAN

Litofiilsete rändkalade liikumismustrid avatud ja tõkestatud jõgedes

Maailma kalaliikidest ligi pool asustab magevett, mis moodustab vaid ligikaudu kümnetuhandiku vee-elukeskkondadest maal. Mageveekalastik on suuresti ohustatud, kuna asub inimtegevuse otseses mõjualas. Üheks olulisemaks ülemaailmselt suureneva mõjuga ohuteguriks on paisude rajamine jõgedele. Paljud kalaliigid on rändelise eluviisiga ja liiguvad perioodiliselt üksteisest kaugel asuvate veekogude või nende osade vahel. Veekogu tõkestatuse puhul võib halveneda või kaduda ligipääs elupaikadele, sealhulgas ainsatele kudemis-, toitumis- ja talvitumisaladele. Liigile vajalikud elupaigad võivad asuda nii seisuveekogus (nt meri, järv) kui ka vooluveekogus. Rändeteid elupaikade vahel on tihti vaid üks (nt kindel vooluveekogu lõik), mistõttu suurte probleemideni võib viia üksainus rändetõke. Eesti võrdlemisi laugest maastikust tulenevalt napib siin sigimiskohta kärestikel kudevatele ehk litofiilsetele kalaliikidele, mispärast rändeteede tõkestatus mõjutab sellise elupaiganõudlusega liike eriti olulisel määral. Võtmeelupaikade hulk on aja jooksul vähenenud, näiteks jõgede paisutamise ja homogeniseerimise tõttu. Leevendusmeetmete tõhusus pole sageli teada, kuna paljude elustikurühmade (nt karpkalalased) käitumist on võrdlemisi vähe uuritud ja see võib piirkonniti erineda.

Käesoleva doktoritöö peamine eesmärk oli kindlaks teha kärestikel kudevate rändeliste kalade liikumise seaduspärasusi jõgedes. Töö baseerub neljal teadusartiklil (I–IV). Uuriti kolme kalaliiki: karpkalalaste tõugja (III, IV) ja vimma suguküpsed isendeid (I) ning lõhe noorjärke (smolte; II). Uuringute läbiviimiseks kasutati akustilist telemeetriat ja erinevaid klassikalisi meetodeid. Akustilise telemeetria puhul varustatakse kalad märgistega, mis saavad perioodiliselt veekeskonda individuaalseid signaale. Märgisega kalu manuaalsete või statsionaarsete jaamadega jälgides koguti detailset infot iga isendi ööpäevaste liikumiste kohta mõne kuu (lõhe), aasta (vimba) või mitme aasta jooksul (tõugjas). Moodustus enam kui miljoni asukohakirjega andmebaas, mida analüüsiti kirjeldamiseks kalade liikumisi ja leidmaks seoseid kala ja tema elukeskkonna parameetrite vahel. Kalu (*Osteichthyes*) uuriti akustilise telemeetria abil Eestis esmakordselt.

Artiklis II uuriti lõhesmolte eluperioodil, mil nad rändavad jõest merre. Laskuvad smoldid pidid allavoolu jõudmiseks läbima Purtse jõe rajatud hüdroelektrijaama kompleksi ja valima kolme võimaliku rändeteede – loodusliku ilmega kalapääsu, liigveelasu ja turbiinikanali – vahel. Hinnati eeskätt rajatud kalapääsu kasutamist, turbiinikanali sissevoolul oleva võre efektiivsust kalade tõkestamisel ja turbiine läbinud smoltide suremust. Iga rändeteede väljavoolul püüti laskuvad kalad mõrraga kinni, et hinnata nende vigastusi ja määrata järelsuremust. Pärnu jõel korraldatud uuringus (I) püüti vimmad nende kudeperioodi algfaasis Sindi paisu alt ja vabastati märgistatuna paisust ülesvoolu. Uuriti kalade käitumist ja kudealade kasutamist hüpoteetilises olukorras, kus nende ülesvoolu ränne poleks olnud paisu poolt takistatud. Märgiste pikk eluiga võimaldas jälgida ka vimmade

kudejärgset merre laskumist, määrata jõkke tagasipöördumise aega, uurida käitumist talvitumisalal ning ööpäevaseid liikumiserütme. Emajões ja sellega seotud veekogude süsteemis uuriti kaitsealuse tõugja rändeid ja ööpäevaseid rütme (III, IV). Eripärane on see, et uuringuala keskmes rändetõkked puuduvad, avalikkus tunneb huvi kaitsealuse liigi piiratud püügi lubamise vastu ja (sarnaselt vimmale) on asurkonna elupaik liigi levila põhjaserva lähedal. Kirjeldati tõugja elupaigakasutuse mitmekesisust ja käitumuslikke eripärasid: koelmu-, toitumis-, talvitumis- ja puhkealade asukohti ning liikumisi nende elupaikade sees ja vahel. Kõigi kolme kalaliigi uuringutulemuste üle (I–IV) arutleti kalabioloogia ja võimalike kaitsemeetmete kontekstis.

Töö tulemusena leiti, et rändelise eluviisiga mageveekalade käitumuslik mitmekesisus ja nõuded elupaiga mõõtmetele võivad olla seni kirjeldatust suuremad. Üksainus rändetõke võib piirata populatsiooni loomupäraselt elupaigakasutust kõigil aastaegadel, iseäranis tõugjal. Ka siis, kui ränded erinevate elupaikade vahel toimuvad harvem, võib ligipääsu vajadus sellele olla obligatoorne (nt koelmualade vähesuse korral). Veekogu loodusliku seisundi halvendamine võib kalastikule kaasa tuua pideva perioodilise ja arvatust kõrgema suremuse (nt turbiinides), isegi siis, kui seadusandlusest tulenevad nõuded on täidetud. Kaplan-tüüpi turbiinide põhjustatud lõhesmoltide suremus oli kokku 36%, kirjandusandmete võrdluses kõrgeim. Kaitsemeetmete rakendamise positiivne efekt võib saabuda väga kiiresti (nt ajalooliste koelmualadele kasutuselevõtt vimmal). Uuringud Purtse jõel tõestasid, et kui laskuvad smoldid on füüsiliselt võimelised kalatõkkevõresid läbima, siis see ka aset leiab. Tuleb arvestada, et paljud kalad rändavad veelgi väiksemate kehamõõtmete juures kui töös uuritud smoldid. Looduslähedased kalateed võivad rändetõkete negatiivset mõju märkimisväärselt leevendada, kuid võimalusel tuleks eelistada siiski veekogu algupärase kalastiku jaoks reeglina sobivaimat lahendust ehk rändetõkete kõrvaldamist.

Töös kirjeldati detailselt karpkalalaste liikumismustreid. Ränded koelmualade suunas leidsid aset väga vara: eelneval sügisel (vimb) või isegi kesksuvel (tõugjas). Nii varane liikumine seisuveest jõgedesse polnud tõugja puhul enne teada. Mõlema liigi talvitumisalad asusid koelmualade läheduses ja võimaldasid vältida ulatuslikke rändeid jahedal ja lühikesel kudemiseelsel perioodil. Võimalik, et see on levila jahedamas servas elavate termofiilsete kalade jaoks oluline, põhjustades ühtlasi senikirjeldatust suuremat erinevust kalade aktiivsuses sooja ja jaheda perioodi vahel. Talvitumisalal vahetasid vimmad asukohta, eriti aktiivselt jääkate lagunemise järel. See, et enamus vimbade peatus kudemisperioodil enam kui ühel koelmualal, võis olla seotud nende portsjonilise kudemisega. Vimbade liikumismustrid koelmualade vahel olid väga varieeruvad. Tõugjas liikus koelmutele ja naases sealt ootamatult madalal temperatuuril – see võimaldas neil ühtlasi varast liikumist toitumisaladele. Toitumisperioodiks laskus enamus tõugjatest (valdavalt suuremad isendid) järve, naastes sealt juba ca 2–3 kuu möödudes jõkke jäänud tõugjate lähedusse, peamiselt Emajõe kesk- ja ülemjooksule. Järvest lahkumise aeg langes kokku toksiliste vetikaõitsengute tüüpilise algusajaga, kuid võis olla seotud ka sihtveekogu hea hüdro-morfoloogilise seisundi ja vanajõgede rohkus-ega, pakkudes kalatoidulise tõugja jaoks soodsaid toitumistingimusi. Tõugjad

kasutasid aasta jooksul ootamatult suurt jõelõiku (keskmiselt 80 km, minimaalselt 40 km) ja liikusid vähemalt nelja Natura 2000 kaitseala vahel, lisaks kaitsestaatuseta aladel.

Ööpäeva lõikes varieerus tõugja aktiivsus märkimisväärselt kogu aasta jooksul, vimma puhul enamikel aastaegadel. Autorile teadaolevalt pole vimma aktiivsuse ööpäevast varieerumist jõgedes kõigi aastaegade jooksul varem kirjeldatud. Tõugja puhul polnud ööpäevase aktiivsuse igakuine varieerumine varem teada. Ööpäevased liikumismustrid erinesid aastaajati, tõugja puhul valdavalt isegi kuude lõikes. Kõigi kuude vältel oli tõugjas aktiivsem hommikul ja/või õhtul. Sarnane aktiivsuse ajastus ilmnes ka vimma puhul. Tõugjas muutus päeval ajal täiendavalt aktiivseks limiteeritud valgustingimustes (oktoober-märts), mitte suvisel perioodil, nagu seni teada. Öhtune aktiivsus kadus hilissuvel ja varasügisel ehk sarnasel perioodil aastast nagu kirjeldatud harrastuskalapüügil Soomes. Uurides kalastiku ruumilist või ajalist varieeruvust Euroopa standardi EN 14757:2015 abil, võib võrreldavate tulemuste saamiseks olla vajalik 24-tunnise püügiperioodi rakendamine.

Kokkuvõtlikult võib rõhutada, et mageveekalastiku mitmekesisuse säilitamine üha suureneva inimõju tingimustes on suur väljakutse, kusjuures oluline on juhtumipõhine lähenemine. Tundes kalade elupaigaspetsiifilist käitumist, saab täpsustada ohutegureid ja suurendada kaitsemeetmete tõhusust. Iseäranis tähtis on see väheuuritud rändelise eluviisiga kalaliikide asurkondade puhul, kelle jaoks olulisemate elupaikade kättesaadavus ja nende kasutamise seaduspärasused ei pruugi isegi teada olla. Teadmistes olevate lünkade täitmiseks pakub telemeetria suurepäraseid võimalusi, saadud tulemused on kõrge usaldusväärsusega.

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Tambets, M., Kärgenberg, E., Thorstad, E. B., Sandlund, O. T., Økland, F. & Thalfeldt, M. (2018). Effects of a dispersal barrier on freshwater migration of the vimba bream (*Vimba vimba*). *Boreal Environment Research*, 23: 339–353.

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