Realia et Realia naturalia

MARTIN KESLER

Biological characteristics and restoration
of Atlantic salmon *Salmo salar* populations
in the Rivers of Northern Estonia

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by the relevant Roman numerals:

I. Kesler, M., Vetemaa, M., Saks, L. & Saat, T. 2013. Survival of reared Atlantic salmon (*Salmo salar*) smolts during downstream migration and its timing: a case study in the Pirita River. *Boreal Environment Research*, **18(1)**, 53–60.

II. Kesler, M., Kangur, M. & Vetemaa, M. 2011. Natural re-establishment of Atlantic salmon reproduction and the fish community in the previously heavily polluted River Purtse, Baltic Sea. *Ecology of Freshwater Fish*, **20(3)**, 472–477.

III. Taal, I., Kesler, K., Saks, L., Rohtla, M., Verliin, A., Svirgsden, R., Jürgens K., Vetemaa, M. & Saat, T. 2014. Evidence for an autumn downstream migration of Atlantic salmon *Salmo salar* (Linnaeus) and brown trout *Salmo trutta* (Linnaeus) parr to the Baltic Sea, **68**, 373–377.

IV. Visse, M., Sild, E., Kesler, M., Saks. L. & Hõrak P. 2015. Do Atlantic salmon parr trade growth against immunity? *Marine & Freshwater Behaviour & Physiology*, **48**, 225–240.

Author's contribution:

The author's contribution to papers **I** and **II** included the generation of the original idea and hypothesis, data collection, data analysis and manuscript writing. For publication **III** the author's contribution constituted of participation in the formulation of the original idea, data collection and commenting on the manuscript. For publication **IV**, the author's main tasks were participating in data collection and the interpretation of results.

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I. INTRODUCTION

The Atlantic salmon (*Salmo salar* L.) is listed in annexes II and V of the European Union's Habitat Directive and the protection of their fresh water rearing areas is incorporated in the Estonian Nature Conservation Act. In its historical distribution area, salmon is an important part of the fish community and its presence an indicator of the high ecological status of rivers according to European Union Water Framework Directive.

Despite their protected status, salmon are still a highly valued resource for commercial and recreational fisheries Salmon fishing in the Baltic Sea catchment area was originally confined to the capture of ascending spawners in rivers or at the coast near the mouths of spawning rivers – a method of exploiting salmon stocks that dominated until the end of the 19th century (Karlsson & Karlström 1994). Between 1915 and the mid-1940s, total annual catches of salmon were approximately 1000 t (Karlsson & Karlström 1994). Thereafter a growing intensity of offshore drift gillnet and longline fishing resulted in an increase in annual salmon catches to approximately 3000 t. High fishing pressure after the 1940s caused a decline in natural recruitment in many rivers that still had intact riverine habitat. Offshore fishing primarily takes place in the main basin of the Baltic Sea, which is the main feeding area for most salmon stocks. Between 1945 and 1990, commercial offshore fishing steadily increased its share of the total salmon catch to about 80% (Karlsson & Karlström 1994). Due to the ban on drift gillnet fishing in 2008 and a reduced quota, the share of salmon caught by offshore fishing has decreased to approximately 20% (ICES 2014). Since the second half of the 2000s annual salmon catches have been 1000 t.

Wild Atlantic salmon populations over the vast majority of this species' distribution area have declined drastically (WWF 2001). In the Baltic Sea region, 70% of historical salmon populations are extirpated. The main causes of declining populations are the loss of spawning habitat (creation of migration obstacles and deteriorating water quality) and overharvesting (HELCOM 2009). The primary method to compensate for declining natural recruitment has been stocking – the release of hatchery-reared juveniles (Karlsson & Karlström 1994). A rapid increase in stocking occurred during the late 1950s and enabled the continuation of intensive salmon fishing despite the negative trend in wild recruitment (Karlsson & Karlström 1994). Since 1987 the average annual number of reared salmon smolts released into the Baltic Sea has exceeded 5 million (ICES 2014). The survival of salmon smolts in the early phase of their first sea sojourn has drastically decreased since the 1990s. Because of declining salmon smolt survival the total allowed catch (TAC) in the Baltic Sea was gradually reduced from 650,000 fish in 1993 to 108,762 fish in 2013 (ICES 2014).

Salmon populations in Northern Estonia have shown similar dynamics to those of other Baltic Sea regions. By the 1990s only four (in the rivers Kunda, Loobu, Keila and Vasalemma) of eleven self-sustaining natural populations in Northern Estonia remained (Fig. 1, Kangur & Wahlberg 2001). As in other areas, the main method of restoring extirpated salmon populations has been the stocking of hatchery-reared juveniles into potentially suitable rivers that had lost their original population. In parallel with stocking, the regulation of fishing and improvement of habitat and water quality were also prioritized. Fish passage past (over, through) anthropogenic migration obstacles is seen as a critical next step to further safeguard endangered migratory fish species (Kangur & Wahlberg 2001). In 2013 wild recruitment occurred in nine Northern Estonian rivers, dough two of the region's biggest rivers (Narva and Jägala) had minor or no wild reproduction (Kangur & Wahlberg 2001; ICES 2014).

Rearing Atlantic salmon to supplement weak or restore extinct populations has been inconsistently carried out in Estonia since the 1930s. Hatcheries have existed in Sindi, Keila-Joa and Narva, however there are no data regarding the outcomes of releases. A systematic stocking programme started in 1997 with the creation of the Põlula Fish Rearing Department that belongs to the Estonian State Forest Management Centre – the hatchery is currently financed by the Estonian Ministry of the Environment. The outcome of the stocking programme is monitored by the Estonian Marine Institute, University of Tartu, via surveying parr densities and gathering catch samples.

Many authors have questioned the rationality of stocking salmonids as a conservation and or fisheries management measure (Fleming & Petersson 2001; Brown & Day 2002). Furthermore, many studies have demonstrated poor survival of stocked fish (Jonsson *et al.* 1991) and potential genetic impacts upon non-target populations (Fleming & Petersson 2001). Survival rates of salmon smolts in the Baltic Sea have undergone considerable declines in recent decades and the rationale for releasing reared juveniles has thereby diminished (ICES 2014). Concern over the viability of hatchery reared fish has been raised on several occasions (Kallio-Nyberg *et al.* 2004; Romakkaniemi 2008). It is generally accepted that wild salmon smolts have higher survival rates during smolt migration and the post-smolt phase at sea than hatchery reared smolts (Jonsson *et al.* 1991; Kallio Nyberg *et al.* 2004). The period after release of hatcher reared smolts and entering the sea is critical in terms of predation (Larsson 1985). It is hypothesized that the timing of migration is a major factor influencing survival of postsmolts (McKinnel & Lundqvist 2000; Kallio-Nyberg *et al.* 2004). Migration of wild smolts occurs during an ecological and physiological "migration window", when the conditions for migration are optimal (Jonsson & Ruud-Hansen 1985; Zydlevski *et al.* 2005). Smolt transformation depends on the cumulative temperature regime

experienced during spring and on changes in day length (Jonsson & Ruud-Hansen 1985; Zydlevski *et al.* 2005). Zydlevski *et al.* (2014) concluded that smolts actively migrate downstream for a month and if they do not reach the sea in that time, they become resident and start to behave as parr again. Only few studies have focused on comparing the behavior of released hatchery reared smolts with wild smolts.

Based on these concerns, the first study quantify the survival of reared salmon during their freshwater migration period and to compares 1- and 2-year old hatchery reared fish. These two age classes are the most common hatchery release groups and the long-term viability of these fish largely determines the effectiveness of hatchery programmes.

Timing of sea entry of released and wild smolts was compared, because any mismatch between optimal and actual down migration timing likely results in poor survival at sea (Jokikokko & Mäntyniemi 2003; Jutila *et al.* 2005). Difference in timing of sea entry between hatchery reared and wild smolts could at least partly explain the poor survival of reared fish during the sea migration period.

Second, this study investigated the development of a salmon population in the formerly heavily polluted River Purtse. Changes in the river's fish community were compared to the improvement in water quality. The two-part hypothesis was that: addressing the main causes behind the extirpation of salmon populations is a precondition to achieving the recovery of a population; the recovery of a salmon population can be effectuated by straying spawners – a process that was preliminary assumed to take decades.

Third, this study describes the phenomenon of autumnal migration of salmon parr to the low saline waters of the Baltic Sea. Due to a lack of information, this aspect of salmon behavior is generally ignored in management decisions. However, this phenomenon may be of considerable importance, *e.g.* in the context of mitigating the effect of migration obstacles. For instance at hydroelectric power stations the safe downstream passage of juveniles is considered important only during spring.

Tradeoffs between immunity and different life history traits in fish have remained largely unstudied. A well-functioning immune system that keeps parasites and pathogens in check is paramount for survival and fitness. However, the development, maintenance and use of the immune system are costly because it requires energy and/or limited micronutrients (Klasing 2004; Martin *et al.* 2008; Sadd & Schmid-Hempel 2009). It was hypothesized that the parameters of immune function correlate with body length and mass, and gonad size. Condition-dependent immune responsiveness assumes that individuals with a higher amount of available resources invest them proportionally to different components of fitness and it was predicted that immune responsiveness correlates positively with indices of physiological condition. Such tradeoffs between immunity and

life history traits in the wild salmon population could serve as an example and justification to maintain genetic variance and complexity of life histories in the hatchery rearing programs. Hatcheries generally focus on producing as large juveniles as possible and rearing practices inevitably lead to homogeny in life history patterns. These changes could lead to reduced immune responsiveness of hatchery reared fish and in turn reduce the long term viability of hatchery programmes.

These research topics were chosen because such aspects of the biology of Atlantic salmon should enable the modification of hatchery practices in order to meet wild population restoration objectives more precisely.

2. MATERIALS AND METHODS

2.1. The study species

Atlantic salmon are an anadromous fish species native to the northern Atlantic Ocean and rivers that flow into the Atlantic. Several isolated populations also occur in the large lakes and seas in North America and Northern Europe. Salmon spawn in river sections with a gravel bottom and swift current, where they create redds (a nest of gravel into which fertilized eggs are deposited). The hatching fry stay in the river from 1 to 8 years (depending on their growth) and are referred to as "parr" (young salmon during their first freshwater phase). When parr reach a certain size (usually over 10 cm), they transform into "smolts" (juveniles adapted to live in saline water). Smolt migration to the sea occurs during spring and at this stage fish imprint the odors of their natal stream to enable them to return to the same river when they have reached adulthood. During the early phases of their sea lives salmon are called "post-smolt". High mortality can occur during the post-smolt life stage. Salmon are known to return to their specific natal river or tributary of a larger river during spawning migration, behavior referred to as homing. Atlantic salmon stay in the sea from half a year to 4 years (depending on food resources and growth rate) before returning to spawn (Jonsson & Jonsson 2011). Salmon in the Baltic Sea do not migrate out from the Danish straits; the main wintering and feeding areas are located in the southern parts of the Baltic Sea (Rannak *et al*. 1983). Unlike salmon species in the Pacific Ocean, Atlantic salmon are iteroparous. Repeated spawners however form a minority of the spawning stock (Jokikokko & Jutila 2005).

Salmon in the Baltic Sea are geographically and genetically isolated from other North Atlantic populations (Koljonen *et al*. 1999). Baltic salmon populations can be divided into northwestern and southeastern phylogeographic lineages. The northwestern (Atlantic) lineage colonized the rivers of northern Sweden and Finland from the west after the last Ice Age. The southeastern (Ice Lake) lineage colonized the Baltic Sea during the Baltic Ice Lake stage from the east. Salmon in the Northern coast of Estonia belong to the southeastern lineage (Koljonen *et al*. 1999).

Historically salmon regularly spawned in 80–120 rivers flowing into the Baltic Sea (IBSFC & HELCOM 1999). Human activities such as damming, pollution and overfishing have decreased the number of rivers salmon spawn in. There currently remain at least 43 rivers that flow into the Baltic in which salmon reproduce. Most of these rivers hold original populations, though some are mixed wild/ hatchery populations owing to stocking (HELCOM 2009).

2.2. The study area

The Baltic Sea is the second largest brackish water basin in the world. It has a horizontal salinity gradient that decreases from the Danish Straits in the west to Bothnian Bay and the Gulf of Finland in the east (Ojaveer & Pihu 2003). In its southern parts surface salinity is 3–12 ‰, while in the Gulf of Finland it varies between 2–6 ‰. Salinity also varies vertically – under the halocline (at a depth of 50–70 m) salinity is 10–22 ‰ (Ojaveer & Pihu 2003). Surface water salinity of the Atlantic Ocean is from 33 to 37 ‰. Due to the low salinity of the Baltic Sea, smolts migrating from the rivers situated around the Gulf of Finland have considerably lower energetic costs during sea sojourn compared to populations inhabiting rivers flowing directly into the Atlantic Ocean.

Compared to other salmon rivers in the Baltic Sea region, those of Northern Estonia are among the smallest in terms of flow volume and catchment area. The 11 rivers that historically hosted salmon populations in Northern Estonia have several similar characteristics that potentially influence the biology of local salmon populations (Fig. 1).

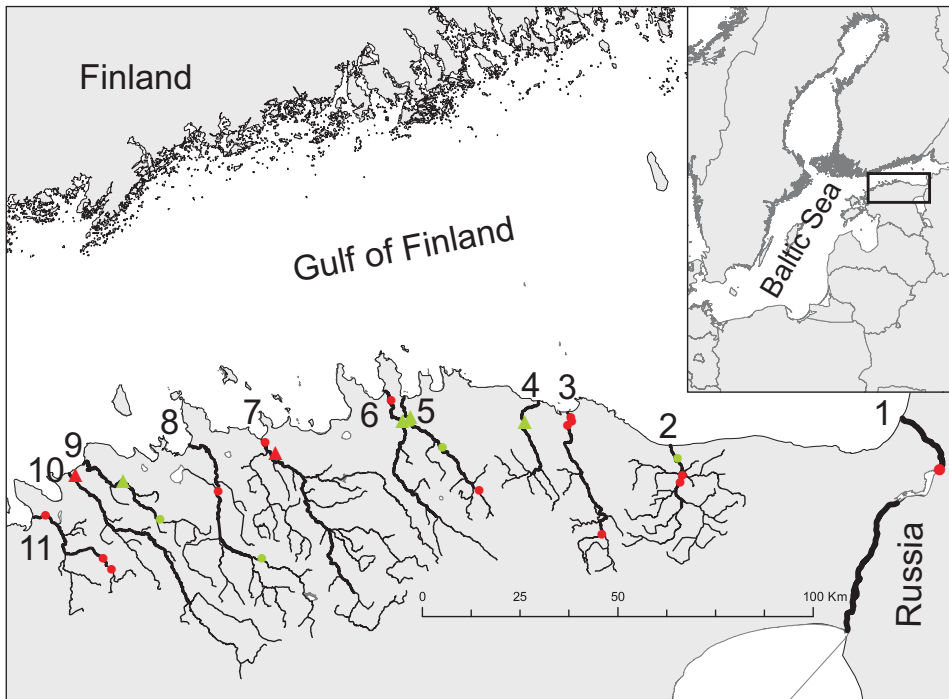**Figure 1.** Rivers with historical salmon populations on the Northern Estonian coast. Numbered rivers are: 1) Narva; 2) Purtse; 3) Kunda; 4) Selja; 5) Loobu; 6) Valgejõgi; 7) Jägala; 8) Pirita; 9) Vääna; 10) Keila; 11) Vasalemma. Waterfalls are marked with triangles and dams with circles. Obstacles with fish passes or that are easily passable to salmon are marked with green and fully or virtually impassable obstacles with red.

The rivers flow from south to north and an area with a high gradient is located on the lower reaches of the rivers. These sections are typically associated with areas of limestone bedrock called the Baltic Klint and represent the largest and most productive spawning and juvenile rearing areas in these rivers. However, in some rivers the limestone bedrock results in waterfalls that are natural migration obstacles to fish. Such waterfalls exist on the Jägala and Keila rivers. All Northern Estonian rivers are relatively short and the river sections accessible to migratory fish not longer than 50 km. A more detailed overview of Northern Estonian salmon rivers is given in Table 1. Because of the short migration distance and relatively small size of the rivers the spawning run usually occurs in late autumn shortly before spawning. River Narva is larger than the others and the spawning run occurred in summer and early autumn (Rannak *et al.* 1983)

Table 1. Main characteristics of the historical salmon rivers in Northern Estonia. Length and catchment area data was sourced from www.keskkonnaagentuur.ee and flow data from Loopman 1979.

River	Length, km	Catchment area, km^2	Elevation at source, m	Average annual runoff (MQ) m^3/s	Minimum amount of flow (NQ) m^3/s
Narva	74.3	56200	30	305–410	70–80
Purtse	51.1	811	77	5–7	0.3–0.5
Kunda	66.3	536	90	5–6	0.7–1.0
Selja	46.4	423	76	2.5–3	0.3–0.4
Loobu	60.6	314	100	2–2.5	0.2–0.4
Valgejõgi	89.4	452	107	2–2.5	0.2–0.4
Jägala	98.9	1481	82	10–12	0.6–1.8
Pirita	106.8	808	75	5–7	0.1–0.4
Vääna	64.3	315	64	3–3.5	0.04–0.1
Keila	111.8	669	75	5.5–6.5	0.2–0.5
Vasalemma	54.1	396	50	3–4	0.1–0.2

2.3. History of the salmon population and oil shale pollution in the River Purtse

The River Purtse (Fig. 1) has historically been noted as one of the most productive salmon rivers in the Northern Estonia. For example, in 1929 the officially registered catches of salmon and sea trout were 4.94 t and 1.15 t respectively (Martinson 1958). The loss of the river's fish community and native salmon population was caused by the development of the oil shale industry. The first mine and processing plant was established in 1918 and rapid expansion of the industry occurred after World War II (Veldre *et al.* 1979).

The oil shale industry has proved to be a significant source of polycyclic aromatic hydrocarbons (Veldre *et al.* 1979), sulphates, chlorides and phenols (Liblik & Rärsepp 1994; Trapido *et al.* 1995). The peak period of pollution of the River Purtse was from 1980–1983, when an estimated 500–800 t of monophenols were released into the river, resulting in concentrations of monophenols in the waters as high as 0.9–2.3 mg/l (Risto *et al.* 2008). This was up to 2300 times higher than the national standard for monophenols in water at that time. A significant reduction in oil shale processing during the 1990s resulted in a corresponding reduction in pollution loads. Since 2000 all wastewater from oil shale processing plants and ash deposition areas is collected and cleaned. These measures resulted in a steady improvement in the water quality of the River Purtse (Fig. 2 and 3). Today the treated wastewater is diverted away from the river and pumped directly into the Baltic Sea. This measure has removed this pollution risk from the River Purtse.

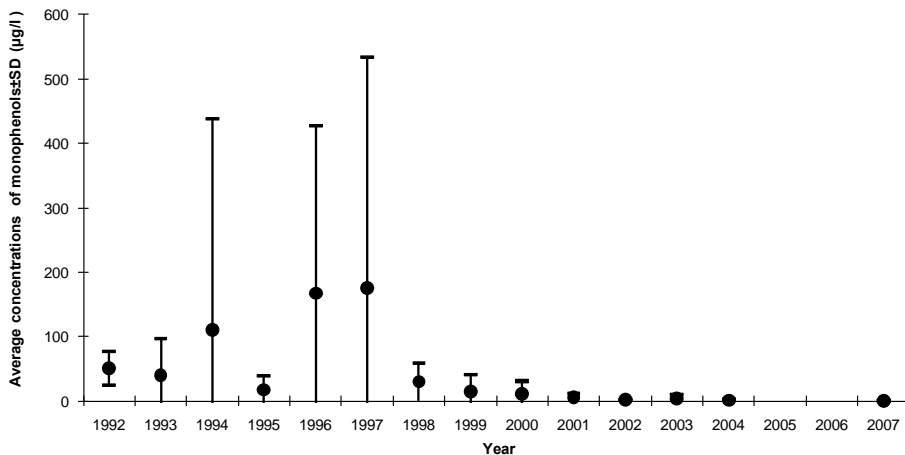**Figure 2.** Average (±SD) concentrations of monophenols in the River Purtse from 1992–2007. In 2005 and 2006 18 samples out of 24 had phenol values <0.5 μg/l, which is below the measureble level (www.keskkonnaagentuur.ee, Paper **II**, Figure 2).
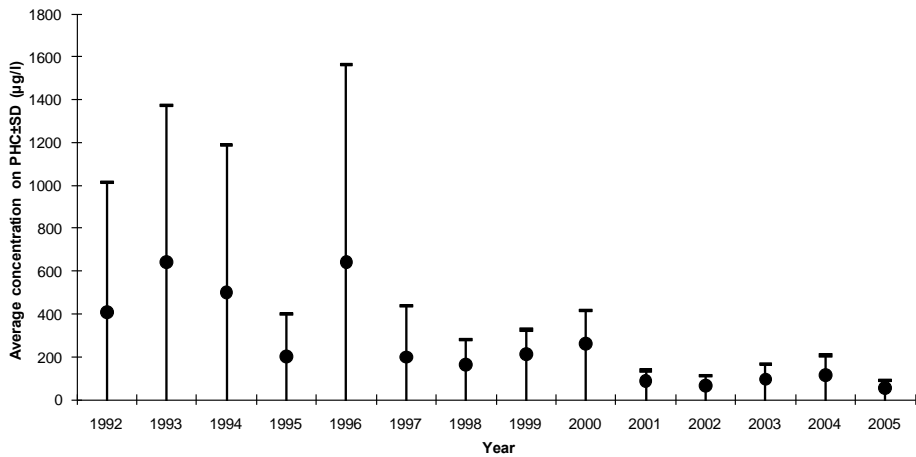
Figure 3. Average (±SD) concentrations of total petroleum hydrocarbons (PHC) in the River Purtse. In 2006 and 2007 all samples had PHC values <50 μg/l, which is below the measurable level (www.keskkonnaagentuur.ee, Paper **II**, Figure 3).

2.4. Field sampling and methods

Hatchery reared smolt samples for survival estimates (Paper **I**) were gathered at the mouth of the River Pirita. The fish were caught using a trap net that covered about 1/3 the width of the river. Trapping started as soon as the river was free of ice and flow conditions enabled the installation of the net. The temperature at the beginning of trapping was below 5 °C. Sampling was terminated in June when no smolts had been caught for three days; water temperature at this time was above 15 °C. All hatchery reared fish had adipose fin clipped, this enabled to distinguish them from the wild fish.

The number of smolts reaching the river mouth was calculated using Petersen's mark-recapture method (Schwartz & Dempson 1994). The fish were caught in the trap, marked with a Visible Implant Elastomer (VIE, Northwest Marine Technology Inc., Shaw Island, USA) tag in the post-ocular tissue and released 2 km upstream from the trap. From the share of re-captured fish, the fishing efficiency of the trap was calculated. The survival of released smolts was estimated by comparing the calculated number of smolts that reached the trap with the amount of fish that was previously released.

Parr density and fish species composition (Paper **II** and **IV**) in the rivers Purtse, Keila and Vasalemma was assessed using electrofishing. The size of each fishing site varied between 300–400 m². To ensure a high capture rate, sites were always fished twice at an interval of 30 minutes.

Autumn migrant parr were collected from Eru Bay in Northern Estonia (Paper **III**). Sampling was carried out with gillnets and hand (beach) seine (see Taal *et al*. 2014 for details). The closest salmon river to the fishing site was the River Loobu – its outlet was 2 km away.

Age and migration pattern of salmon were determined from sagittal otoliths. Before chemical analysis, otoliths were ground from the sulcus side until the core area and primordium became visible. Otolith strontium to calcium ratios (Sr:CA) were quantified with laser ablation inductively coupled plasma mass spectrometry (Paper **III**).

The immune responses of 2-summer old parr was studied in Paper **IV.** The fish were captured from the Vasalemma and Keila rivers. Oxidative burst in whole blood samples was measured using an ABEL® Cell Activation test kit with Pholasin and Adjvant-K^{TM} (Knight Scientific, Plymouth UK) according to the protocol of Sild & Hõrak (2010).

2.5. Statistical methods

In Paper **I** the effect of age on the survival of stocked fish during migration was calculated using a chi-square (χ^2) test on smolt counts of different origin. Separate generalized models (GLM) with logit link were used to test the effect of origin (released 1-year old fish which had remained in the river for an additional year compared with wild smolt) and age (released 1-year old fish compared with released 2-year old fish) on the individual descent time. In paper **II** comparison of the total length of young-of-the-year salmon between the River Purtse and River Kunda during a study period (2006–2009), a nonparametric Mann–Whitney U-test was used. In paper **IV** the recorded variables were normally distributed, hence parametric methods (t-test, Pearson's correlation and ANCOVAs) were used for data analysis. Study site was always included in ANCOVAs as a two level factor. Because testing multiple hypotheses required performing several tests on a number of measured traits (many of which were interdependent), we set a study-wide α-level of 0.001 for significance of two-tailed tests. Un-adjusted p-values were also reported.

3. RESULTS AND DISCUSSION

3.1. Survival of reared smolts during the descent to the sea

In the River Pirita, the majority of 2-year old hatchery reared smolts migrated to the sea within a week of release (Paper **I**). In contrast 1-year old hatchery reared smolts delayed their migration to the sea for up to a month (Fig. 4). Some of the released 1-year old fish stayed in the river as parr for another year. The migration timing of these staying individuals coincided with that of wild fish during the following spring (Fig. 5), which indicates that river conditions prior to transformation in to smolts determine the timing of smolt migration. Even though there was significant annual variation, average river survival of 2-year old smolts was in the range of 33.0–58.6%. The survival of 1-year old smolts was considerably lower at 17.0–20.6% (Paper **I**).

Smolts of both age groups were reared in the same hatchery in near identical conditions. The difference in behavior between 1- and 2-year old smolts therefore indicated that they responded differently to the environmental factors that triggered their transformation into smolts and migration behavior. This knowledge has practical implications for improving hatchery practices. Smolt releases are generally favored over parr releases, because it is assumed that released smolts migrate downstream shortly after release and are therefore less reliant on the feeding and habitat conditions in the river. That is why smolts are typically released at a single site and in large numbers (Brown & Day 2002). The behavior of 2-year old smolts (Fig. 2) and the results of previous studies (Jonsson *et al*. 1990; Jokikokko & Mäntyniemi 2003) affirm this concept. Based on our work however these assumptions do not seem valid in the case of 1-year old smolts (Paper **I**). The significant delay in migration observed by us could lead to crowding and high mortality after release. Crowding created by reared smolts could also negatively influence wild juveniles in the release areas. One way to reduce such a potential negative effect would be to release 1-year old fish at multiple sites and in smaller groups, though this would make the release procedure considerably more labor intensive. The second option might be to choose a release site without wild fish, however this would require detailed and up-to-date knowledge on the distribution of wild fish. If these options are not available, releasing 1-year old smolts might not be practical.
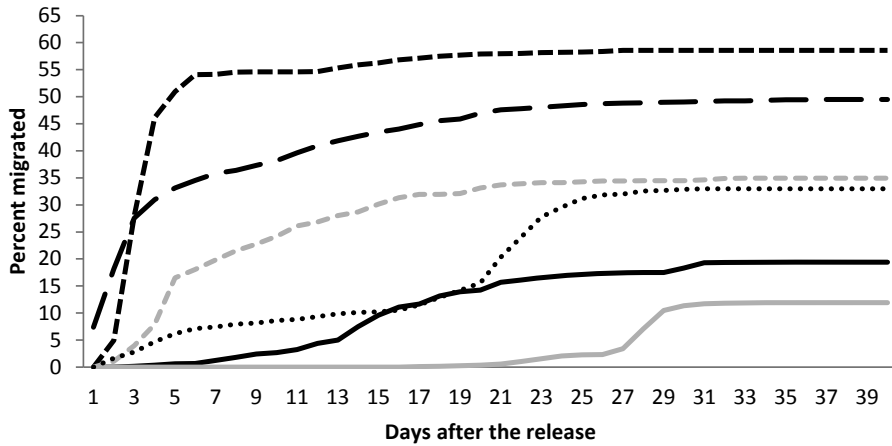
Figure 4. Estimated cumulative share of the released hatchery smolts (- - - 2Y in 2007, – – – 2Y in 2008, - - - 2Y in 2009, ⋯⋯ 2Y in 2010, –– 1Y in 2007 and –– 1Y in 2009) that reached the smolt trap in River Pirita (Paper **I**, Figure 2).
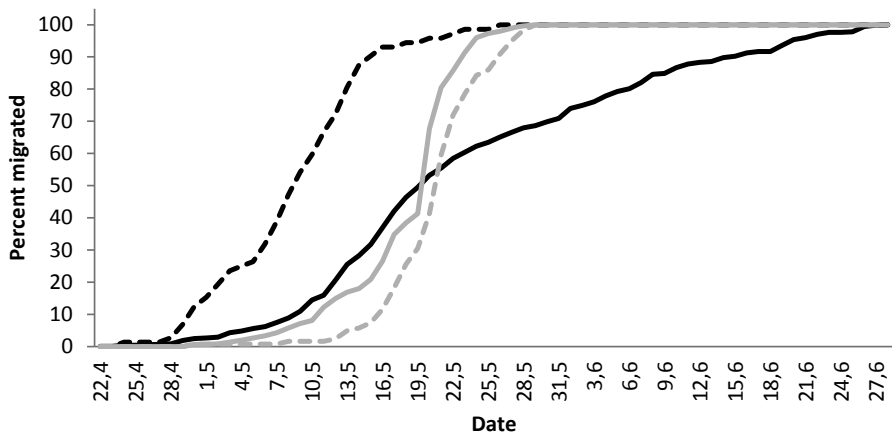
Figure 5. Estimated cumulative share of the released hatchery fish that remained for an additional year in the river and wild smolts (- - - reared fish in 2008, ––– wild fish in 2008, - - - reared fish in 2010, –– wild fish in 2010. 100% equals the total number of fish captured) that reached the smolt trap at the mouth of the River Pirita (Paper **I**, Figure 3).

As the salmon rivers in Northern Estonia have quite similar characteristics and the released fish originated from a single hatchery, it is likely that the presented migration and survival patterns are valid for all Northern Estonian Rivers. The results however should be applied with caution to other regions as Atlantic salmon generally inhabit considerably larger rivers, the hatchery practices may differ greatly and or fish of different origin may exhibit different behavior and life history strategies.

3.2. Recolonization of a historical salmon river

During the 1990s the River Purtse was considered not suitable for restoration of a naturally reproducing salmon population (Paper **II**). In 2000s the water quality started to improve and irregular electrofishing surveys indicated that the original fish composition started to recover (Paper **II**). The first documented spawning of salmon and anadromous brown trout occurred in the River Purtse in 2005. In that year all caught spawning salmon had a clipped adipose fin, *i.e.* they originated from a hatchery (Paper **II**). There were no previous releases of salmon to the River Purtse and therefore the observed fish must have strayed from other rivers. The closest stocked rivers were the Selja and Narva, 37 and 60 km away respectively. During the following year (2006), a modest amount (6.8 individuals per 100 m^3 of riverbed) of young-of-the-year salmon parr were found at a site located 4 km from the river mouth (Paper **II**). Parr were also found during the following three years (2007–2009), indicating that the straying of spawners from other rivers occurred repeatedly. In conclusion, the results of Paper **II** demonstrate that once a suitable spawning habitat becomes available, salmon are able to colonize it in just five years.

The main goal of the Estonian hatchery programme is to increase the amount of spawners to enhance reproduction in the wild. Higher numbers of fish (wild or hatchery reared) also increases the potential number of adults that may stray to other rivers. Some studies note that hatchery reared fish stray more than their wild conspecifics (Jonsson *et al.* 2003). The higher straying rate of hatchery fish could be explained by releases to the sea or river mouths, which may provide insufficient time for fish to memorize the river's water chemistry (Quinn 1993). Straying also could be higher if smolts are released too late during the migration season. In this case fish might be already imprinted to the water of the rearing site and not to the release site (Quinn 1993). All releases in Northern Estonia during the last few decades have been done into the river, usually several kilometers upstream from the sea. Releases are also scheduled to match the beginning of natural smolt migration. Therefore the risk of straying is kept at a minimal level.

Salmonids generally home to their natal sites to spawn (Quinn 1993). This results in numerous local micro-adaptations and inbreeding at a population level (Quinn 1993). It seems that the scarcity of strays and or low spawning success of straying fish are the reason why there are numerous genetically distinct locally adapted populations (Quinn 1993). This is consistent with the translocation of salmonids being notoriously unsuccessful (Quinn 1993), particularly so in the case of Atlantic salmon. Therefore straying as a potential factor in stock recovery processes has generally been ignored.

The ecological mechanisms responsible for straying and the colonization of unoccupied areas are not well described. However, straying seems to be an

integral part of the evolutionary biology of salmonids (Quinn 1993). Variation in the chance of straying among populations and species appears to be due to behavioral and geographical differences (Quinn 1993). Jonsson & Jonsson (2003) reported an average straying rate of wild Atlantic salmon (over the time period 1976–1999) in the River Imsa (Southern Norway) of 5.8%. Annual straying rates varied significantly from 0% to 23%. Length of sea-sojourns correlated positively with straying rate; two-sea-winter fish had an almost two times higher straying rate than one-sea-winter fish (Jonsson & Jonsson 2003). The vast majority of strayed fish entered rivers that were less than 60 km from their natal river and more fish stayed in rivers that held larger populations (Jonsson & Jonsson 2003). The straying rate of released fish in the same study was 15.4% (Jonsson & Jonsson 2003). Hatchery fish were released very close to the river mouth (less than 100 m) and thus poor imprinting was probably the cause of the observed difference. However, it seems that hatchery reared fish do not necessarily have higher straying rates than wild conspecifics Johannsson *et al.* (1998) reported a 2.1% straying rate for reared fish which homed to a hatchery in Iceland, which is notably smaller than for wild fish in the River Imsa. Jonsson & Jonsson (2003) suggested that where Atlantic salmon stray into neighboring coastal rivers to spawn a meta-population structure could be formed. The recolonization of the River Purtse seems to fit this concept, because DNA profiles of salmon parr showed clear similarities in neighboring rivers and with the fish in the regions only hatchery that releases salmon (Gross *et al.* 2014). Straying also suggests that abundant populations form a source for the recovery of neighboring populations in rivers of previously poor status.

3.3. Parr autumnal downstream migration

Paper **III** illustrates that some salmon in Northern Estonia migrate downstream in the autumn as parr and are not restricted to estuaries during winter. The parr sampled in this study were caught over 2 km from the nearest river with a salmon population. This is the first such documented behavior for Atlantic salmon (Paper **III**). It seems that autumn descending Atlantic salmon parr are able to survive and thrive in the brackish Baltic Sea (salinity in the Gulf of Finland is 2–6 ‰, which is lower than the average for the Baltic Sea). It has been shown that 6–7 ‰ salinity is not a physiological obstacle for the survival of brown trout parr (Landegren 2001), a species closely related to Atlantic salmon.

Juvenile salmon migrate to the sea in spring as smolts. Transformation to smolts prior to sea entry is critical for survival in saline environments (Hoar 1988). However, some authors (Cunjak *et al.* 1989; Pinder *et al.* 2007) have also reported autumnal downstream movement of Atlantic salmon parr. Riley

et al. (2008) concluded that autumn migrating Atlantic salmon parr are not yet physiologically adapted to saline water and expected salmon parr survival in the Atlantic Ocean to be very poor. It has been shown that salmon parr tend to winter in estuarine habitats where salinity is low enough for them to survive (Cunjak *et al.* 1989; Pinder *et al.* 2007). Ibbotson *et al.* (2013) hypothesized that the mechanism triggering autumn migration includes both intrinsic factors such as size and position in the dominance hierarchy, and extrinsic factors related to the supply of food, shelter availability and the presence of predators, such as density and habitat.

It could be hypothesized that autumnal migration is characteristic to the brackish water bays of the Baltic Sea and might play an important role in the overall abundance of Atlantic salmon in the region. The spawning and parr habitat arear in the rivers of Northern Estonia are typically located on the lower and middle stretches of rivers. Therefore downstream migration to the sea is short and probably requires relatively little effort. Pinder *et al.* (2007) highlighted that in the River Frome in Southern England up to 25% of the spring salmon smolt run originated from fish that had wintered in the estuary as parr. Mark and recapture studies carried out in this river also indicated that autumn migrant parr contribute to the returning spawning cohort (Riley *et al.* 2009). Therefore autumnal migration could be a viable life history trait, particularly in the context of the brackish waters of the Baltic Sea.

3.4. The effect of parr growth and maturity on immunity

Paper **IV** compared the immune response of mature male parr with juvenile female parr in two of Northern Estonia's completely native salmon populations (those of the Keila and Vasalemma rivers). Maturation of male two-summer old parr seemed to be common in both studied populations; only one juvenile male parr was identified during sampling of forty fish. Our study revealed no difference between mature males and juvenile females in the capacity of phagocytes to produce oxidative burst. This result clearly refutes the hypothesis that precocious male parr suffer higher depletion of bodily reserves and immune suppression compared to juvenile females of the same age and size. This finding is notable in the context that gonadal tissue of male parr comprised 13–24% of total body mass. Data seemed to indicate that investment into gonadal tissue did not have a significant cost in terms of decreased immune system performance. One possible explanation for this is that male parr have to pass a "threshold" to enter the reproductive stage; this threshold results in a bodily condition that is comparable to non-reproductive females of the same age. Such an explanation is compatible with

the findings that onset of maturation in male Atlantic salmon parr is triggered only when body size and fat reserves exceed certain threshold values (Myers *et al.* 1986; Rowe *et al.* 1991). Nonetheless it was surprising that body condition of reproductive males and non-reproductive females were similar in present study, given that the attainment of maturity can reduce growth and survival in male Atlantic salmon parr (Jones & Hutchins 2001). One possible explanation of the similar body conditions in present study is that faster growing females had already left the river as 1-year olds. Therefore, staying slower-growing female parr were similar in size to mature male parr. This hypothesis is supported by Mitans (1973), who noted that females dominated among 1-year old smolt groups. Our results also suggest that the costs of reproduction are primarily associated with spawning effort, rather than the preceding spermatogenesis *per se*.

Male parr may become mature before migrating to the sea and it has been shown that such individuals can mate with high success (Johnstone *et al.* 2012). Mature male parr increase the effective population size considerably, enabling populations to maintain higher genetic variability (Johnstone *et al.* 2012). Such a life history trait however can result in higher mortality compared to juvenile (male and female) parr, which in turn may result in a lower number of anadromous male spawners (Mitans 1973). Based on the abundance of parr in different age classes and male parr maturity rate in the River Salaca (Latvia), Mitans (1973) concluded that the mature male parr had a 57.1% survival rate compared to juvenile parr of the same age class. This resulted in a female-biased sex ratio of 1:1.3 in the anadromous part of the population. The sex ratio of anadromous spawners in the River Pirita was 1:1.25 in favor of females (Kesler *et al.* 2015). A female-biased sex ratio among anadromous part of the populations is a clear indicator of the presence of mature male parr.

Northern Estonian salmon populations are small, with the effective population size of anadromous spawners currently estimated to be in the hundreds or a maximum of a few thousand. For example 191 wild and 28 hatchery spawners ascended the River Pirita in 2014 (Kesler *et al.* 2015), one of the largest salmon rivers in the area. Nevertheless these small populations have been able to maintain their own genetic diversity (Paaver *et al.* 2001).

Present study found a significant negative correlation between parr length and immune response (Paper **IV**). Such a correlation indicates a trade-off between immunity investment and growth, with growth taking priority over immune responsiveness in some individuals and *vice versa*. This suggests that fast growth and larger size is not always a guarantee of improved survival or fitness in the wild. The general policy of hatcheries to produce the largest juveniles as possible may therefore not be as efficacious as previously thought. Although studies demonstrate that larger hatchery reared smolts have better survival (Hansen 1988;

Saloniemi *et al.* 2004). Nevertheless wild smolts have considerably higher survival compared to hatchery reared smolts, despite of their smaller average size (Saloniemi *et al.* 2004). Wild smolts have also less evident size dependent trend in survival (Saloniemi *et al.* 2004). This suggests that hatchery reared smolts are poorly adapted to live in the wild and large size helps, to some extent, compensate this.

Tradeoffs between growth and other physiological attributes are also interesting in a broader context. The evolution of anadromous behavior among salmonids suggests that with specialization, species tend to have shorter fresh water residency and smaller smolt size (Quinn & Myers 2006). For instance two of the globally most abundant and anadromous salmon species (pink *Oncorhynchus gorbuscha* and chum *Oncorhynchus keta*) leave spawning freshwaters as fry shortly after hatching and therefore small smolt size can be a favorable evolutionary trait (Groot & Margolis 1991). Higher mortality of smaller smolts during their early lives at sea may be compensated for by higher net production of smolts. It has generally been implied that the availability of freshwater spawning and rearing habitats are the determining factors regulating the abundance of anadromous salmonid species. Density dependent survival in freshwater has been repeatedly demonstrated (Jonsson *et al.* 1998; Armstrong & Griffiths 2001).

4. CONCLUSIONS

1. The release of 2-year old hatchery reared smolts appears more effective way to increase the amount of spawners than the release of 1-year old smolts. Due to the shorter residency of 2-year old smolts in rivers, the negative influence (crowding in suitable habitat) upon wild juveniles is likely smaller. The migration timing of hatchery reared smolts in the River Pirita differed considerably from wild fish and this may result in the poorer survival of released fish at sea. There was also a significant difference in river survival between released 2- and 1-year old smolts.

2. The releasing of salmon at parr stage is a potential way to produce smolts that resemble wild fish in behaviour, especially if there is empty habitat available in the river. Some released 1-year old fish stayed in rivers for an additional year and migrated to the sea the following spring. The sea entry of these fish coincided with wild smolts, who migrate during the optimal period and this is a beneficial attribute.

3. The recovery of the River Purtse salmon population suggests that any restoration effort should prioritize improving the most critical conditions (such as water quality, habitat availability and migration possibilities) and employment other measures (such as reared juvenile releases) are of secondary importance.

4. The autumnal migration of parr to the brackish waters of the Gulf of Finland may have a more significant role than previously thought regarding the overall abundances of local salmon populations. This phenomenon must be taken in to account during planning and management decisions. For instance, the hydroelectric power stations that operate on salmon rivers should also provide safe downstream passage for juveniles during autumn.

5. Hatchery programmes nearly always focus on the fast growth of fish. However, fast growth and larger size is not always a guarantee of improved fitness in nature. Salmon populations of the Keila and Vasalemma rivers had a significant negative correlation between immune response and parr growth.

SUMMARY IN ESTONIAN

Lõhi (*Salmo salar*) populatsioonide bioloogilised iseärasused ja taastamine Põhja-Eesti jõgedes

Lõhi looduslike populatsioonide arv ja arvukus on drastiliselt vähenenud praktiliselt kogu leviala ulatuses. Läänemere piirkonnas on ligikaudu 70% algsetest populatsioonidest hävinud. Peamisteks põhjusteks on kudejõgedele rändetõkete rajamine, halvenenud veekvaliteet jõgedes ja ülepüük. Seetõttu on liigi loodusliku järelkasvu esinemine kujunenud oluliseks indikaatoriks jõeelustiku ökoloogilise seisundi hindamisel. Lõhi on kantud Euroopa Liidu Loodusdirektiivi teise ja viiendasse kategooriasse, Eesti ohustatud liikide punase nimestiku esimesse kategooriasse ning liigi taastootmisalade kaitse magevees on integreeritud Looduskaitseseadusesse. Rangetele kaitsemeetmetele on paralleelselt lõhi endiselt hinnaliseks töönduslikuks püügiobjektiks. Möödunud sajandi esimesel poolel toimus Läänemere piirkonnas lõhepüük valdavalt kudejõgedes või rannikul jõesuudmete läheduses ning aastane saak püsis 1000 t tasemel. Sajandi teises pooles kujunes peamiseks triivvõrgu ja jadaõngepüük avamerel. Ajavahemikul 1945–1990 moodustas avamerepüük ligikaudu 80% lõhe kogusaagist, mis püsis suurusjärgus 3000 t. Samal ajaperioodil hoogustus lõhi noorkalade asustamine, mis võimaldas püügisurvet säilitada, kuigi populatsiooni looduslik taastootmine oli juba siis langevas trendis. 2000-ndatel vähenes avamerepüügi osakaal 20%-ni ning aastane saak langes 1000 tonnini. Väljapüügi languse peamiseks põhjuseks oli meres toituvate noorkalade kõrge loodusliku suremuse tõttu vähendatud püügikvoot. Avamerepüügi osatähtsust vähendas ka triivvõrkude keelustamine 2008. aastal.

Põhja-Eestis on lõhi ajalooliselt siginud üheteistkümnes jões, kuid 1990-ndate lõpuks olid populatsioonid säilinud kõigest neljas jões. Põhja-Eesti kudejõgede veekvaliteedi ja rändetingimuste parandamise kõrval on lõhi arvukuse taastamisel suurt tähelepanu pööratud ka noorkalade asustamisele potentsiaalselt olulistesse jõgedesse. Selleks rajati 1997. aastal Lääne-Virumaale Põlulasse kalakasvandus (praegu RMK kalakasvatusosakond).

Töös uuriti kasvanduse päritolu lõhi laskujate ellujäämust ja merre ründe ajastust võrrelduna looduslike laskujatega. Uuring viidi läbi Pirita jõel aastatel 2007–2010. Valdav enamus kaheaastasena asustatud laskujatest rändas merre nädala jooksul peale asustamist. Kaheaastased laskujad asustati jõkke enne looduslikku laskumisperioodi ning nad jõudsid merre siis, kui loodusliku päritolu kalade laskumine alles merre algas. Asustatud üheaastaste laskujate merre ründe oli oluliselt aeglasem ning selle ajastus kattus suuremal määral looduslike kaladega. Kaheaastaste asustatud laskujate ellujäämus oli jõeründe jooksul keskmiselt 44%, üheaastastel seevastu vaid 19%. Osa aastasena asustatud kaladest ei rännanud

kohe merre, vaid jäid järgmise kevadeni jõkke ning laskusid siis üheaegselt koos looduslike laskujatega. Uuringu põhjal võib soovitada, et üheaastaseid kalu tuleks edaspidi jõkke hajusamalt asustada. Samuti tuleks asustamisel eelistada jõelõike, kus looduslikku päritolu kalu ei esine või nende arvukus on madal.

Klassikaliseks näiteks lõhi asurkondade kadumisest on Purtse jõgi, mis on ajalooliselt olnud Põhja-Eesti üheks suurimaks lõhijõeks. Jõe valgala asub Ida-Virumaa põlevkivi kaevandamise ja töötlemise keskmes. Põlevkivitööstuse kahjulike kõrvalsaaduste loodusesse lekkimise tulemusena hakkas jõe veekvaliteet halvenema juba 1920-ndatel, mistõttu suri kohalik lõhipopulatsioon välja. Reostuskoormuse tipp-perioodiks oli 1980–1983, kui jõkke juhiti ainuüksi ühealuselisi fenoole 500–800 t. Veekvaliteet hakkas paranema 1990-ndatel, kui jõe valgalal olev põlevkivitööstus vähenes ning senisest märgatavalt rohkem hakati tähelepanu pöörama keskkonnakaitsele. Esimest korda märgati Purtse jões kudevaid lõhisid 2005. aasta sügisel. Kõikidel tabatud kudevatel isenditel oli rasvauim lõigatud – niisiis oli tegu teistesse jõgedesse asustatud kasvanduse päritolu kuderändel kalade eksimisega Purtse jõkke. Imsa jõe näitel on teada, et kõige tõenäolisem on lõhide eksimine kodujõe suudme läheduses asuvatesse naaberjõgedesse. 2006. aastal tabati Purtse jõest samasuvised lõhitähnikuid, millest järeldub, et lõhi suutis jões looduslikult sigida. Seega ei peaks Põhja-Eesti lõhijõgesid rangelt erinevateks populatsioonideks lugema, vaid lähestikku asuvad sarnase hüdroloogiliste ja morfoloogiliste tingimustega jõgedes elutsevad lõhid moodustavad pigem teataval määral omavahel seotud metapopulatsiooni. Uuringu tulemustest järeldub, et kui looduslike populatsioonide taastamisel tagatakse head sigimis- ja elutingimused on lõhi suhteliselt kiiresti võimeline sigimisalad looduslikult taasasustama.

Jões elavad lõhitähnikud on enamasti paikse eluviisiga, talvitudes jõesuudmetes või jõega ühenduses olevates sobilikes järvedes ning laskudes alles piisava suuruse saavutamisel kevadeti merre toituma. Siiski on täheldatud, et osa tähnikuid rändab oma senistest elupaikadest allavoolu juba sügisel. Põhjusteks on pakutud talvitumispaikade vähesust või suur asustustihedust ja/või kisklust jões.

Töö tulemusena dokumenteeriti esmakordselt tähnikute sügisene allavoolu ränne ka Läänemere lõhijõgedes. Vastandina senisele infole (et talvituvad tähnikud jäävad jõe vee mõjualasse) ilmnes, et Eru lahes võivad tähnikud rännata ka jõesuudmetest eemale. Kuigi senine teaduskirjandus väidab, et sügiseti allavoolu rändavad tähnikud ei ole veel soolases merevees elamiseks kohastunud, näib, et riimveelise Läänemere lahtede madal soolsus ei ole lõhi noorjärkudele füsioloogiliseks takistuseks. Sellist käitumist võib soodustada asjaolu, et Põhja-Eesti jõgede alam- ja keskjooksudel paiknevatelt peamistelt taastootmisaladelt on mereni väga lühike maa. Kirjeldatud nähtus on tõenäoliselt omane teistelegi Läänemere madala soolsusega piirkondadele ning seda tuleks edaspidi lõhevarude hindamisel

arvesse võtta. Tähnikute sügisese rändega tuleb arvestada ka lõhijõgedel asuvate hüdroelektrijaamade töörežiimide kavandamisel. Lisaks kevadisele rändeperioodile võiks edaspidi ka sügisel rändavate noorkalade turbiinidesse sattumise vältimiseks rakendada vastavaid kaitsemeetmeid.

Viimase doktoritöösse kaasatud uuringu käigus hinnati immuunreaktsiooni tugevust Keila ja Vasalemma jõest pärit kahesuvistel tähnikutel. Juveniilsete emaste ja nn. kääbusisaste (tähniku elustaadiumis suguküpsuse saavutanud isendid) immuunreaktsiooni tugevuse võrdlemisel olulisi erinevusi ei leitud. Teadaolevalt on kääbusisastel juveniilsete tähnikutega võrreldes suurem suremus, kuid tõenäoliselt on see seotud kudeperioodi ning sellele järgneva talvega. Koelmutel võivad kääbusisaste suremust kasvatada ka väiksemaid konkurente eemale peletavad suured anadroomsed isased. Kudemisel kulutatud energia tõttu võib kääbusisastel järgneval talvel energiareservidest puudu jääda, mis ongi ilmselt kõrge suremuse peapõhjus. Immuunreaktsiooni tugevuse ja tähniku suuruse vahel ilmnes oluline negatiivne korrelatsioon. See tulemus on mõnevõrra vastuolus üldise arusaamaga, et suurematel noorkaladel on parem ellujäämus ning üldine kohasus. Uuringust tuleneb, et tulevikus jõgedesse asustatavate noorkalade käitumine ja mõõtmed võiks olla võimalikult sarnased kohalike looduslike kaladega, vastupidiselt senisele arusaamale, kus asustatavate tähnikute maksimaalset suurust peetakse peamiseks kvaliteedikriteeriumiks.

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