Eesti Maaülikool
Estonian University of Life Sciences

THE ESTIMATION OF STOCKED AND NATURAL EUROPEAN EEL (*ANGUILLA ANGUILLA*) POPULATIONS IN ESTONIAN WATERS

ANGERJA (*ANGUILLA ANGUILLA*) LOODUSLIKE JA ASUSTATUD POPULATSIOONIDE ARVUKUSE HINNANG EESTI VEEKOGUDES

PRIIT BERNOTAS

A Thesis
for applying for the degree of Doctor of Philosophy
in Applied Biology

Väitekiri
filosoofiadoktori kraadi taotlemiseks
rakendusbioloogia erialal

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, referred to in the text by the relevant Roman numerals. Papers are reproduced with kind permission from the publishers.

I **Bernotas, P**., Vetemaa, M., Saks, L., Eschbaum, R., Verliin, A., & Järvalt, A. (2016). Dynamics of European eel landings and stocks in the coastal waters of Estonia. *ICES Journal of Marine Science: Journal Du Conseil*, *73*(1), 84–90. https://doi.org/10.1093/icesjms/fsv245

II Silm, M., **Bernotas, P**., Haldna, M., Järvalt, A., & Nõges, T. (2017). Age and growth of European eel, *Anguilla* (Linnaeus, 1758), in Estonian lakes. *Journal of Applied Ichthyology*, *33*(2), 236-241

III **Bernotas, P**., Öğlü, B., & Nõges, P. (2020). How do environmental factors affect the yield of European eel (*Anguilla anguilla*) in a restocked population? *Fisheries Research*, *230*, 105649.

IV Tambets, M., Kärgenberg, E., Järvalt, A., Økland, F., Kristensen, M. L., Koed, A., & **Bernotas, P.** (2021). Migrating silver eels return from the sea to the river of origin after a false start. *Biology Letters*, *17*(9), 20210346.

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INTRODUCTION

Over the last 50 years, similar to other parts of Europe, Estonia has witnessed declining European eel (*Anguilla Anguilla)* populations in both coastal and freshwater ecosystems. This study concentrates on analyzing the factors affecting these eel populations through long-term datasets, scientific sampling, restocking initiatives, and environmental variables. European eels' decline has been attributed to overfishing, habitat loss, parasites, pollution, and oceanic changes, and in 2007, the European Council implemented Regulation No 1100/2007 which aims for the recovery of eel stocks in Europe by reducing the anthropogenic mortalities and ensuring a 40% escapement rate of silver eels compared to pre-anthropogenic influence levels. Estonia's coastal eel fishery has mirrored the overall European trend, experiencing a decline in commercial and recreational landings since the 1970s. The reduction in licenses for specialized eel fishing gear, such as small fyke nets, contributed to diminished landings while the number of large fyke net licenses has remained constant, indicating a potential decline in the eel stock, further supported by scientific monitoring. Eel restocking is a widespread management strategy in Europe, including Estonia. This study analyzes the efficacy of restocking in Lake Võrtsjärv, identifying optimal conditions for growth, such as restocking densities, environmental factors, feeding conditions, and developmental stage while restocking. Our investigation also sheds light on the migratory patterns of restocked eels. While capable of migrating from freshwater to saline waters, some eels exhibit unexpected behaviors, returning to their rivers of origin and spending prolonged periods in freshwater before resuming migration. The results of this study aim to contribute to the ongoing debate surrounding the decline of European eel, help understand the underlying factors behind the decline in the northeastern corner of eels' area of distribution, and offer new information on restocked eels' growth and migratory patterns.

1. REVIEW OF LITERATURE

European eel (*Anguilla anguilla*) is one of the most discussed fish species in the world whether by conservationists or fishermen alike. Eel has a unique life cycle among fishes, divided between different development stages and habitats. Eels are known to spawn in the Sargasso Sea in the Atlantic Ocean after which the eel larvae are known as *leptocephali*. Using ocean currents the *leptocephali* drift toward the European coast where they transform into glass eels and the eels' continental life phase begins. The next stage in the eels life cycle is known as the elver phase where pigmentation and habitat selection take place. After settling down eels enter the yellow eel stage which also accounts for the main growth phase. When the yellow eels reach sexual maturity, triggered by hormonal changes and environmental cues, they undergo further physiological transformations. This phase is called the silver eel stage where eels' appearance changes in preparation for their downstream migration back to the Sargasso Sea to spawn (Tesch et al., 2003).

Eel stock has been in decline for decades and remains still very low compared to the levels of the 1960s-70s, which are widely regarded as the reference of a healthy stock. As eels are spread from North Africa and the Mediterranean to Scandinavia the decline has affected fisheries and ecosystems all over Europe with the time frame being similar. The sharpest drop in recruitment happened in the 1980s and the reasons for the decline are numerous.

Fisheries

Eels are related to fishing mortality in every life stage from glass- to silver eel. Glass eel fisheries are concentrated in countries where most of the recruitment occurs – France, the UK, Spain, and Portugal. French glass eel fisheries have been active since the 19th century and developed in effort and capacity for most of the 20th century (Briand et al., 2007). The commercial landings for glass eels in Europe peaked in the 1970s due to improved fishing practices and rising international demand. Glass eel landings started to drop in the 1980s due to a sudden decline in recruitment and diminishing profitability of the fishery (Briand et al., 2007). In 38 years, European glass eel landings have declined from 2000 t (1980) to 60 t (2018; ICES, 2020a).

Eels in the yellow and silver stage are fished all over Europe and while some countries (Belgium, Denmark, Germany, Greece, France, Italy, Portugal, Spain, UK) have distinguished fisheries for either stage, other countries (Estonia, Finland, Latvia, Lithuania, Netherlands, Poland, Sweden, Turkey) have mixed fisheries where stages are not differentiated (ICES, 2020a). Ireland and Norway have closed all eel fisheries since 2010. Outside of Europe, there are substantial commercial fisheries for eel also in Morocco, Tunisia, and Egypt. Yellow- and silver eel landings have dropped from roughly 10,000 t at the beginning of the 1980s to 2700 t in 2018 (ICES, 2020a). According to the latest complete commercial fisheries records (2017), the biggest eel landings were reported in France (434 t), the Netherlands (422 t), the UK (322 t), Denmark (257 t), Italy (214 t), Poland (173 t) and Tunisia (149 t; (ICES, 2020b).

Eels are also a popular target for recreational fishermen in many European countries. However, laws for recreational fishing gear, fishing effort, specimen bag limit, data collection, etc. vary by country making a clear assessment of the impact of recreational fishing difficult (Hanel et al., 2019; ICES, 2020c). A study undertaken in France (Baisez and Laffaille, 2008) showed that recreational anglers may land around 500 t of eel a year while the official records report no data at all (ICES, 2020b).

Within every fishery, there are always illegal, unreported, and unregulated landings (IUU). However, due to insufficient data, the impact of IUU on the eel stock is unknown (ICES, 2020a).

Habitat loss

Habitat loss can relate to complete loss of habitat, inaccessibility, or reduced accessibility of habitats or degraded habitats (ICES, 2020a). Inaccessibility or reduced accessibility of habitats is perhaps the most discussed of the aforementioned factors. The main problem here is the inability to reach upstream in riverine systems as glass eels or elvers and the migration back to the sea in the yellow or silver eel stage (ICES, 2020a). This holdback of migration is connected to the presence of different barriers (such as dams, weirs, sluices, etc.) on suitable waterways (ICES, 2020a). The potential impact of the constrained upstream migration besides the inability to reach suitable habitats

includes increased glass eel mortality below the barriers (White and Knights, 1997; Mouton et al., 2011).

Habitat may be lost also due to amelioration, especially in the West European coastal areas where drainage and abstraction of waterways have led to the loss of wetlands, which have been described as good-quality eel habitats (Dekker, 2003).

Parasites

One of the discussed reasons behind the decline of eel stocks in Europe is the spread of parasites, most notably *Anguillicoloides crassus*. *A. crassus* is thought to have been derived from eels imported to Europe from Asia at the beginning of the 1980s (Lefebvre et al., 2013; Wielgoss et al., 2008) and has been spreading rapidly since its introduction. For example, in Estonian lakes over 50% of the eel population are infected with the parasite (ICES, 2020a; Kangur et al., 2010). The parasite itself invades the swim bladder wall and lumen and can cause inflammatory reactions, hemorrhages, fibrosis, bleeding, or a total collapse of the organ infected (Lefebvre et al., 2013; Molnár et al., 1993; Würtz et al., 1996). Although there is no concrete evidence that infected eels are not able to complete the spawning migration there is a strong possibility that the physiological effects of swim bladder infection reduce eels ability for a demanding migration towards the Sargasso Sea (Kirk, 2003).

Pollution

It has been found that most contaminants (apart from some specific spills or accidents where a large amount of toxic substances are discharged into water) do not have a direct lethal effect on eels (Geeraerts and Belpaire, 2010). Pollution is linked to the decline of eels through chronic sublethal effects of contaminants, which through accumulation in the eel fat tissue can affect spawner quality (Geeraerts and Belpaire, 2010). Spawner quality refers to the capacity of silver eels to reach spawning areas and produce viable offspring (ICES, 2006). As eels are long-lived species and spend prolonged periods in certain habitats they are exposed to constant accumulation of contaminants where pollutants are present (Geeraerts and Belpaire, 2010). The studied contaminants concerning eel quality include dioxins, furans, dioxin-like polychlorinated biphenyls, various metals, and also emerging chemicals

such as brominated and fluorinated compounds (Belpaire et al., 2019; Geeraerts et al., 2011). Assessing the overall impact of pollution on the population of eels is exceedingly difficult due to the eurytopic behavior and specialized biology of the species. The process of oceanic mating and the subsequent distribution of larvae to freshwater habitats are believed to occur in a completely random manner. As a result, it is challenging to establish direct connections between reduced recruitment in polluted freshwater habitats and embryo-larval toxicity caused by maternally transferred contaminants (Belpaire et al., 2019), however, evidence from other species (for example compared to the North Sea whiting *Merlangius merlangus*) suggest that a substantial number of eels are at risk of degrading ability to reproduce (ICES, 2010).

Oceanic changes

When oceanic changes are mentioned in the context of the decline of eel stocks the main connection between the two are the movement of currents (Castonguay et al., 1994), relations between glass eel recruitment and North Atlantic Oscillation (NAO) and water temperature in Sargasso sea (Bonhommeau et al., 2008; Durif et al., 2011; Friedland et al., 2007) or food availability for the leptocephalus larvae on their migration towards European coast (Bonhommeau et al., 2008; Hanel et al., 2014; Knights, 2003). Eel abundance can depend on both the climate-related changes at the time of spawning as well as during the oceanic migration of larvae (Durif et al., 2011). Increased currents toward the North Atlantic may escalate the possibility of a risen number of larvae being distributed in the polar gyre before the metamorphosis, which results in low recruitment in northern Europe (Durif et al., 2011).

Eel Regulation

In 2007 European Council (EC) implemented EC regulation No 1100/2007 (European Council, 2007), which meant establishing measures for the recovery of the stock of European eel. One of the main outputs (Article 2) of the Eel Regulation was the establishment of national Eel Management Plans (EMP) with the objective of each EMP being the reduction of anthropogenic mortalities to guarantee the escapement to the sea of at least 40 % of the silver eel biomass relative to the best estimate of escapement that would have existed if no

anthropogenic influences had impacted the stock (European Council, 2007). However, Eel Regulation states this aim should be achieved in "the long term" and no specific timeline for the 40% achievement of the biomass target is set (EU, 2020a). Within EMPs, different measures to reduce the impact of commercial and recreational fishing, effects of physical obstacles on migration routes, improvisation of habitat, use of restocking to improve the escaping silver eel biomass, target predator control, etc. have been incorporated to reach the targets set (EU, 2020b). The evaluation of the Eel Regulation showed that during the 10-year time frame since its implementation, some progress had been made in reducing fisheries-related mortality. However non-fisheries related anthropogenic mortality has not decreased significantly (EU, 2020b). It is also found that the Eel Regulation itself is rather uncertain concerning the non-fisheries related mortalities, which is why the future eel conservation efforts should concentrate on prioritizing the reduction of aforementioned mortalities (EU, 2020b).

History of eel fisheries in Estonian Waters

Historically, eels have been one of the most important commercially fished species in Estonian waters. Before World War II, hundreds of tons of eel were caught annually from the coastal waters and inland lakes (Kint, 1940). In the 1930s eel fishing in the coastal areas was so profitable, that it attracted fishermen from different Estonian fishing districts. This was mostly due to the estimated landings of freshwater fisheries being much lower compared to coastal fisheries. During the period 1931-1938, the average annual catch from freshwaters was 6.75 t while in the coastal fisheries, it was almost 350 t (Kint, 1940). There is no data available from the World War II period but the coastal landings started to decline in the 1950s (Järvalt, 2008) and continued to drop until the 1990s when for a short period an increase was observed, which was followed by another decline in the beginning of 2000s, which continues to present day (Bernotas et al., 2016). With the construction of Narva Hydropower Station (HPS) at the beginning of the 1950s a large habitat of Lake Peipsi Watershed (surface area approximately 47800 km^2) was cut off as elvers were not able to pass upstream through the HPS dam (Järvalt, 2008; Kangur, 1998). However, to maintain a historic eel fishery an eel restocking program was implemented in Lake Võrtsjärv with the first restocking taking place in 1956 (Järvalt, 2008). Restocking has been regular (with a few off years) since the 1970s and

depending on the year either glass eels or elvers (or both) have been restocked. The number of specimens restocked has fluctuated with the peak in numbers occurring at the end of the 1970s and the beginning of the 1980s when around 2.3 million specimens were restocked annually (Järvalt, 2008). As there is no natural way for eels to reach L. Võrtsjärv the commercial landings of eel depend directly on the volume of restocking. The aforementioned peak in restocking numbers was followed by a peak in eel landings when in 1988 over 100 t of eel was caught from L. Võrtsjärv (Järvalt, 2003). Since the beginning of the 2000s eels have been restocked also into the small lakes of the Peipsi watershed area (L. Saadjärv, L. Kaiavere, L. Kuremaa, and L. Vagula). Eel restocking is financed by fishermen (2/3^{rds} of the total amount, paid by a fraction of the fishing rights fee) and public sources (1/3rd of the total amount, paid with finances from the Estonian Government and the European Maritime and Fisheries fund).

Estonian EMP was compiled in 2008 and implemented in 2009. The EMP divided Estonia into two eel management units (EMUs; (Järvalt, 2008)) – West Estonian River Basin District (RBD) and Narva RBD. West-Estonian RBD covers the western part of Estonia including coastal waters and islands. Two main river systems are located within the EMP – River Kasari and River Pärnu (Järvalt, 2008). While eels were occasionally restocked to the waterbodies of the West-Estonian RBD up to the 1990s the details about these events are relatively unknown. This is why the West-Estonian eel stock is considered natural meaning it consists of natural recruits inhabiting the coastal waters. Commercial fishermen use mainly different types of fyke nets and gill nets in the coastal fishery. Usage of long lines is almost non-existent (landings averaging 8 kg per year in the last decade). The goal of the EMP was to reduce the number of eel-specific fishing gear (small fyke nets set in line) licenses by 50% in the West-Estonian RBD by 2013 (Järvalt, 2008), which was met in 2013 with the number of small fyke net licenses diminishing from 4830 in 2008 to 2414 in 2013.

In Narva RBD the 40% escapement target deriving from the Eel Regulation was set in the EMP (Järvalt, 2008). As mentioned earlier, the eel population of Narva RBD consists of restocked specimens in the freshwater lakes (most notably L. Võrtsjärv) of the RBD.

2. AIMS OF THE STUDY

The main objective of the present thesis was to investigate the factors that have affected the Estonian eel population in both coastal and freshwaters. For this specific hypothesis were formed:

1. Aside from the overall decline of the eel stock, a combination of factors, including historical underreporting, changes in fishing pressure, gear quality, and government policies led to the decline in total landings of eel in Estonian coastal waters (I).
2. The faster growth rates of eels in Lake Võrtsjärv compared to those in smaller lakes in the Narva River Basin are primarily driven by the abundance of Chironomus spp. larvae, but may also be influenced by other factors such as water temperature, population density, and lake productivity (II)
3. Different factors such as the prevalence of cyanobacteria or abundance of meta zooplankton during the time of restocking can influence the commercial yield and thus the biomass of yellow eels in Lake Võrtsjärv (III)
4. A significant number of silver eels that initially migrate to the Baltic Sea return to their freshwater origin before continuing their migration to the Sargasso Sea. (IV)

3. MATERIALS AND METHODS

Study area

Coastal sea

Our coastal study area consisted of 4 districts: Gulf of Finland (ICES subdivision 32), Gulf of Riga (ICES subdivision 28-1), Baltic Proper (ICES subdivisions 28-2 and 29-2) and Väinameri (ICES subdivision 29-4) (Figure 1).

The Gulf of Finland (29 600 km^2) covers the eastern part of the Baltic Sea, from the north-western corner of Estonia to the Neva Bay in Russia. The mean depth of the gulf is 38 m (HELCOM, 1996) and the trophic level varies between mesotrophic in the western part and eutrophic in the eastern part of the gulf (Pitkänen et al., 2008)

Figure 1. Areas of collected samples/data (locations 1-11) and release spot of tagged eels (location 12). 1 – Saarnaki, 2 – Kihnu, 3 – Kõiguste, 4 – Käsmu, 5 – Matsalu, 6 – Vilsandi, 7 – Lake Võrtsjärv, 8 – Lake Kuremaa, 9 – Lake Kaiavere, 10 – Lake Saadjärv, 11 – Lake Vagula, 12 – Narva reservoir.

The Gulf of Riga has a surface area of 16330 km^2 and is adjoined by Estonia and Latvia (Kotta et al., 2008) and is connected to the Baltic proper and Väinameri. The gulf is rather shallow with a mean depth of 27 m, and has a well-mixed water column, resulting in a relatively good oxygen regime. Due to the turbulence and vertical mixing the water transparency is rather low. The benthos-related invertebrate and fish species have formed substantial populations in the gulf (Kotta et al., 2008).

Väinameri (also known as The Sea of Straits or West Estonian Archipelago Sea) is a shallow semi-enclosed area between the islands of Saaremaa, Hiiumaa, and Muhumaa, and the western coast of the Estonian mainland. It's the smallest of the study areas with a surface area of 2243 km^2. Väinameri is very shallow with depths from 3-8 meters prevailing (Suursaar et al., 2001). Despite its small surface area, Väinameri has a large number of different biotopes and a rich benthic diversity (Orav-Kotta et al., 2004).

The Baltic proper fisheries concern the south-western, north-western, and western coasts of the islands Hiiumaa and Saaremaa.

Lake Võrtsjärv

Võrtsjärv is a large, but shallow, eutrophic, and turbid water lake. The surface area of the lake is 270 km^2, making it the second-largest lake in the Baltic States (Järvet, 2004). Its drainage basin (3374 km^2) is situated in the Central Estonian depression of preglacial origin and is connected to the drainage basin of Lake Peipsi (47800 km^2) through the outflowing Emajõgi River (Järvet, 2004). The small mean and maximum depths, 2.8 m and 6.0 m, respectively, make Võrtsjärv responsive to environmental changes. The water is alkaline and due to turbidity, the visibility is low. The lake is covered with ice on average for 135 days, lasting from November until April (Tõnno et al., 2016). No significant trends in the ice cover duration were found (Nõges and Nõges, 2014). According to the Water Framework Directive typology, Võrtsjärv is a large calcareous shallow lake with most ecological status parameters falling into either the "good" or "moderate" class (Tuvikene et al., 2011) During the ice-free period, Secchi depth does not exceed 1 m. Phytoplankton is dominated by eutrophic and highly shade-tolerant cyanobacteria from the genus *Limnothrix* (Janatian et al., 2020). According to the long-

term annual phytoplankton primary production (208 ± 27 gC m^{-2} $year^{-1}$), Võrtsjärv is close to the nutrient-saturated production boundary for lakes determined by latitude where light limitation has the leading role (Nõges et al., 2011).

River Narva

River Narva (400 m^3s^{-1}) draws its water from Lake Peipsi and discharges into Narva Bay, the Gulf of Finland. The basin of the river is 56 200 km^2 with 63% belonging to the Russian Federation, 30 % to Estonia, and 7% to Latvia (Piirsoo et al., 2010).

Fisheries

Coastal fisheries

There has never been a yellow- or silver-eel-specific fishery in Estonia, all fisheries are oriented towards both. However, size limits apply for the catch. The lowest legal size of the eels caught in the coastal sea is TL=35 cm and for inland waterbodies (excluding L. Võrtsjärv, L. Peipsi, and L. Lämmi where the limit is 55 cm) the size limit is TL=50 cm.

Professional eel fishing gear in Estonian coastal waters mainly consists of different-sized fyke nets (mouth sizes up to 3 meters) and smaller fyke nets set in line. It has to be mentioned that in large fyke nets (mouth more than 3 m) eel is mostly regarded as by-catch (1% of total catch) and thus not significant (Järvalt, 2008). That is the reason why this kind of gear can't be counted as specialized eel fishing gear. Fishermen who specialize in eel fishing use mainly special smaller-sized fyke nets (typically set in line) or long lines. The amount of small fyke net licenses in active fishing has been reduced by 50% over the period 2009-2014. Long-lining is professionally carried out only to a very small extent (1.7 kg of eel reported in 2014). However, recreational fishermen use long lines with 100 hooks per line as the main gear for eel fishing. Up to 100 hooks (300 hooks for recreational fishermen residing on small islands with permanent settlements) per line and one line per recreational fisherman is allowed by the Estonian Fishing Law (https://www.riigiteataja.ee/en/eli/503092014004/consolide).

Inland fisheries

Lake Võrtsjärv

One lamprey species (*Lampetra planeri*) and 31 fish species permanently inhabit Võrtsjärv (Järvalt, 2003; Pihu, 1998). Eel, pikeperch (*Sander lucioperca*), pike (*Esox lucius*), and bream (*Abramis brama*) are the most important commercial species in the lake, while perch (*Perca fluviatilis*) and burbot (*Lota lota*) are of secondary commercial interest (Järvalt, 2003; Nõges et al., 2018).

The eel production of Võrtsjärv is entirely based on the restocking of glass eels or elvers. The restocking program started in 1956 and has continued to the present day. Since 1980, the restocking of eel has been annual (excluding years 1986, 1989, 1990, and 1993; Bernotas et al., 2019). The number of restocked individuals has been dependent on available financial resources and thus directly connected to the glass eel market prices (Bernotas and Silm, 2019a). Eel is targeted by commercial fishery using fyke nets (mesh size in the cod end = 18 mm) with the legal landing size being TL ≥ 55 cm. Commercial harvest is due to the legal size dominated by female yellow eels. The number of fyke nets used by the fishermen has stayed at a stable level (from 300 to 360) since 1971(Nõges et al., 2018). The eel fishing season lasts from April to October. No data on the number of fishermen or companies is available for the period before 1990s. The number of fishermen or companies operating the gear has changed during the last 10 years due to companies selling some of the licenses however the number of gears has stayed the same (N=322).

River Narva

According to records, 35 different fish species have been caught from River Narva. However, commercially is the most important River lamprey (*Lampetra fluviatilis*) which is being caught from the downstream of the river using cone-shaped gear (Feršel and Tuvi, 2010). Substantial eel fisheries existed on River Narva at the beginning of the 20th century, when thousands of specimens were caught annually (Vasilyev, 1974). Nowadays there is no commercial eel fishing on River Narva apart from occasional bycatch in the lamprey fisheries.

Data

Four main data sources were used in this study. First, the catch registered by professional fishermen. These include information on the date, gear type, fished species, and weight (kg) of the catch by the ICES subdivision and statistical rectangles (ICES, 1977). These records are collected by the Ministry of Agriculture on a monthly basis and are available in electronic form from 2008 onwards. Most data deficient periods are the late 1980s and early 1990s as some records are missing from that interval and the overall reliability of the data from that period is questionable. The database obtained from the Ministry of Agriculture contained entries for eel catches over the period 2008-2014. Each record featured information on the catch area (ICES – subdivision and statistical rectangle), county of the report, type of gear, harbor, month, and the size of the catch. The catch data concerning the soviet period (1969-1991) was obtained from the databases of the Estonian Marine Institute. The second source used in the study was the recreational fishing database operated by the Ministry of Environment (https://kala.envir.ee/). This comprised data on all of the recreationally fished Estonian waters and has entries dating back to 2008. The information includes fishing date and gear, fished species, and volume of the catch (kg). In the present study, the CPUE was calculated and the fishing effort (100 hooks a night) was separated from the data.

The second source is the data collected by the Estonian Marine Institute. Small fyke nets were used for annual coastal eel monitoring. The gear is 55 cm high with a semi-circular opening and a leader or wing that is 5 m long. Fykes are made of 17-mm mesh in the arm and 10-mm in the cod-end with yarn quality no 201/12 in twisted nylon. Mostly yellow eels were caught using this gear. The average fishing effort for each area/year was 161 fyke days (1 day = 24 h soaking time). Catch per unit of effort (CPUE) data is presented as an average number of eels caught per fyke/day by study years and monitoring areas.

The third and fourth sources are data collected by the Estonian University of Life Sciences. The eel otoliths used in this study date back to 1999. Based on life stage at stocking (glass eel or elver), the otoliths collected from the eels of Võrtsjärv were divided into two groups. The glass eel group contains otoliths collected during the period 1999 - 2003. The elver group includes otoliths from the period 2010 – 2012.

All individuals were caught by professional fyke nets (mesh size > 16mm in the cod end). The eels were measured for total length (TL, cm) and total weight (TW, g), also the date of catch was recorded.

The data on water chemistry, phyto- and zooplankton biomass has been available since 1964 and is collected at least once per month (Nõges et al., 2018). Benthic macroinvertebrate (BMI) samples are taken during the ice-free period and sampled alive, processed using 70 % alcohol, and then dried and weighted (Kangur et al., 1998). The collected data on BMI were converted into total biomass.

For tracking eel movements in River Narva acoustic telemetry was used. Methods are described in detail in paper IV.

4. RESULTS AND DISCUSSION

The decline of the coastal eel fisheries

Our results indicated a strong negative correlation between the studied years and total landings of the commercial fishery in the coastal regions of Estonia during the period 1969-2014 with a similar trend appearing in the catches of the recreational fishery for the period 2005-2012 and scientific monitoring with small fyke nets from 1998-2013 (Figure 2, **I**).

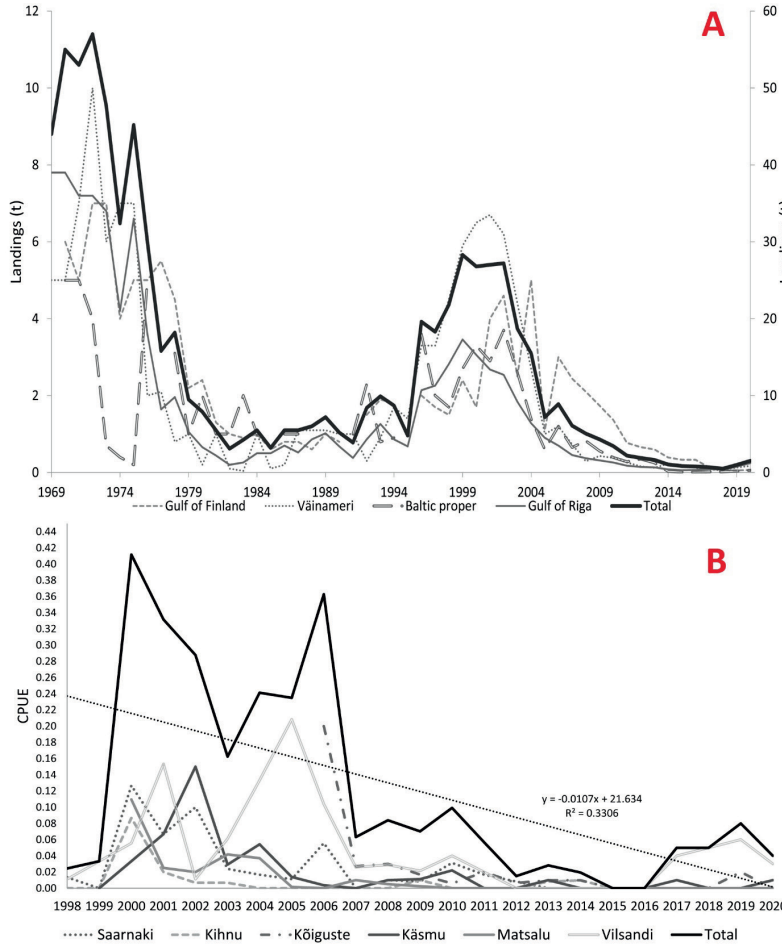

Figure 2. Total landings of eel (in tons) in 1969–2020. The "Gulf of Riga" and "Total" graphs correspond to the scale on the right (A) and Estonian Marine Institute monitoring data (cpue, N/fyke day) for small fyke-nets from 1998–2020. Figure updated and modified from **I**.

A questionnaire, which was carried out among 50 individual coastal fishermen showed that during the 1980s, approximately 40% of the coastal eel catch went unreported (**I**). However, with the change of government at the beginning of the 90s the fishing pressure, quality of the fishing gear (Vetemaa et al., 2006), and registering of the catches increased resulting in a rise in the commercial landings of eel in the coastal waters (**I**). After bottoming out in the 1980s, commercial landings peaked in 1999 (28.3 t) but have declined drastically since the beginning of the 2000s. A similar pattern can be observed in most of the member states surrounding the Baltic Sea and while the decline of the European eel stock is the main driver behind the diminishing landings, reducing commercial fishing effort also plays a role. Since 2008 the landings of small fyke nets in particular dropped sharply with the main reason being reduced effort as well as the diminishing profitability of using such gear (I). The bulk of the eels (81%-93% during the period 2008-2020) from the coastal areas were caught using larger fyke nets however these are not constructed specially for eel fishing and eel is being considered as by-catch to other, more abundant species (such as perch, smelt, pike, roach etc.). As opposed to small fyke nets, the number of large fyke net licenses has remained unchanged during the aforementioned period. As eels are not specially targeted by large fykes the changes in the eel landings can also reflect the changes in the coastal eel biomass.

There is a significant correlation between the CPUE of the monitoring of small fyke nets and commercial landings during the period 1998-2020 (r_s=0.60, N= 23, p=0.002).

Growth of eels restocked in the inland lakes

Our results showed that eels residing in different freshwater lakes of the same region have various growth parameters. Eels inhabiting L. Võrtsjärv showed faster growth rates and higher Fulton K values compared to specimens populating the small lakes in Narva RBD (Figure 3, **II**). Growth rates can be tied to different biotic and abiotic factors, most notably feeding conditions (Edeline et al., 2005; Simon, 2007), population density (Tesch et al., 2003), water temperature (Simon and Dörner, 2014), lake productivity (Shiao et al., 2006; Simon et al., 2013), origin and stage at restocking (Bisgaard and Pedersen, 1991; Lin et al., 2007; Pedersen et al., 2017; Simon et al., 2013).

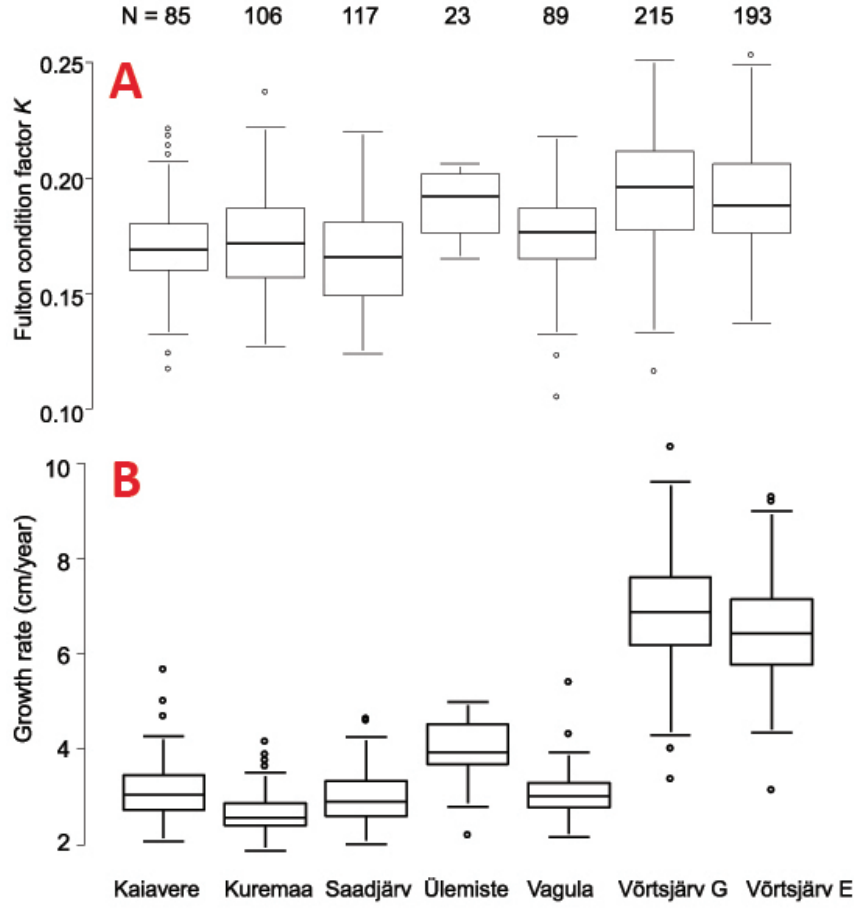

Figure 3. Mean parameters of *Anguilla* captured in different periods (Kaiavere 2010–2012; Kuremaa 2002–2012; Saadjärv 2000–2012; Ülemiste 2003–2004; Vagula 2001–2012; Võrtsjärv G 1999–2003; Võrtsjärv E 2010–2012) in selected Estonian lakes: A – calculated Fulton condition factors (K), B – differences in growth rates. Box = 25% and 75% quartiles and median; bars = maximum and minimum values in analyzed samples. Figure modified from **II**.

In L. Võrtsjärv the main food source for eels is Chironomus spp. larvae (Kangur et al., 1999; Teesalu, 2019), which is very abundant in the lake (Kangur et al., 2004). Apart from L. Kaiavere, the small lakes of Narva RBD are stratified (Ott, 2016a), which can contribute to hypoxic conditions in benthic habitats. Oxygen levels in the hypolimnion however affect the bottom-dwelling chironomid larvae and their distribution in the water body (Heinis and Davids, 1993), making the aforementioned small lakes inferior habitats to Chironomus spp. larvae compared to L. Võrtsjärv. It has been also found that in L. Saadjärv the prevalence of Chironomus spp. larvae amidst the eel diet were lower

than other macroinvertebrates (*Odonata* and *Gammaridae;* (Teesalu, 2019).

Restocking densities during the study period (1999-2012) also varied between the lakes, with L. Võrtsjärv having the lowest number of specimens restocked per hectare annually (N=12, **II**). However, in the small lakes, the mean number of specimens restocked per hectare ranged from N=21 in L. Vagula to N=58 in L. Kaiavere (**II**). Higher eel densities increase competition for food, which induces faster depletion of suitable prey such as insect larvae, making smaller eels switch their diet to fish, reducing body growth (De Leo and Gatto, 1996; Tesch et al., 2003). Apart from feeding competition, population density affects also sources of stress such as the spreading of diseases (Lafferty and Holt, 2003), which can affect the growth rates of fish.

Stratified water columns and possible hypoxic conditions of the small lakes affect the food sources of eels, and they also influence the well-being of eels themselves. Eels are more tolerant to hypoxic conditions than many other species of fish (Farrell and Richards, 2009; McKenzie et al., 2003; Perry and Reid, 1992) however prolonged periods (from weeks to months) of hypoxia in the hypolimnion of the small lakes (excluding L. Kaiavere; (Ott, 2016b) can affect the stress levels of eels deriving from having to switch habitat or food sources for survival. While hypoxia may also occur in the bottom layer of Lake Võrtsjärv due to hot and wind-free periods in summer (Järvet, 2004) the duration of such an event is likely shorter compared to the stratified small lakes.

It is known that the eel growth rate is also connected to the productivity of the habitat (Lin et al., 2007; Poole and Reynolds, 1996). All our studied lakes can be categorized as eutrophic, meaning they are nutrient-rich and have high productivity.

We can assume that the growth rate expresses the welfare of the fish as it is tied to environmental stressors and a slow growth rate can be a sign of chronic stress (Huntingford et al., 2006).

We found that in L. Võrtsjärv, eels restocked as glass eels grew 0.4 cm faster per year than eels restocked as elvers (**II**). This result is comparable with studies carried out by German researchers (Simon et al., 2013; Simon and Dörner, 2014) and shows that the stage at the time of restocking influences the growth rates of eels also in Estonian

habitats. In the small lakes, all eels restocked were assumed to have been restocked as elvers due to the restocking program of the early 2000s where only elvers were released into the inland waterbodies of Estonia so comparison between different stages at restocking was not possible. The lower growth rates of eels in the small lakes were once more verified in 2018 (ICES, 2019) with results being similar to our study (**II**).

Our results showed that the water body where to restock eels should be selected carefully to obtain the best growth conditions as these can reflect on the welfare of the eels and stress-related impairment of growth can also interfere with maturation (Huntingford et al., 2006). In the case of Estonian lakes, the stratified water bodies should be avoided for restocking of eels completely. Well, mixed eutrophic lakes, rich in abundance of Chironomus spp. larvae would be best suited for restocking eels in terms of growth rates, however, the restocking densities should be kept low to prevent unnecessary stress deriving from increased food competition and spreading of diseases.

Which factors influence restocked eels during the introduction to the water body and the yellow eel phase?

According to our results, the prevalence of cyanobacteria has the strongest negative impact on the eels at the time of restocking (Figures 4 & 5, **III**).

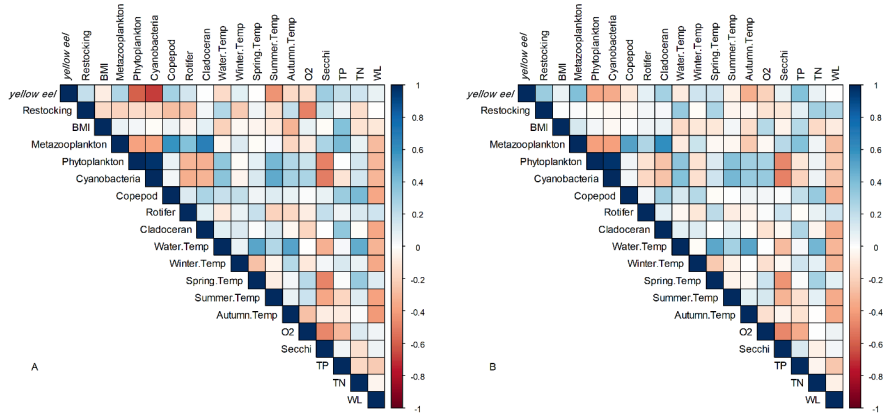

Figure 4. Pearson correlation of the commercial eel yield with restocking numbers and environmental variables during the YOY stage (7 years before the catch; A) and in the year of catch (yellow stage; B). Blue gradients indicate positive correlations and red gradients indicate negative correlations while the intensity of the gradient expresses the correlation strength (**III**).

While the exact impact related to the restocking activities such as transport and release to a water body is unknown, increased vulnerability to environmental stressors in glass eels can be expected. There are no direct studies available on the relationship between cyanobacterial abundance and glass eels however there is evidence concerning other species of fish. The presence of cyanobacteria can decrease the feeding of pike larvae on zooplankton (Engström-Öst et al., 2006). The low nutritional value of cyanobacteria affects the quality of zooplankton through food-web interactions where cyanobacteria-fed zooplankton can be a poor food source for planktivorous fish (e.g., larval stages of fish; (Karjalainen et al., 2007).

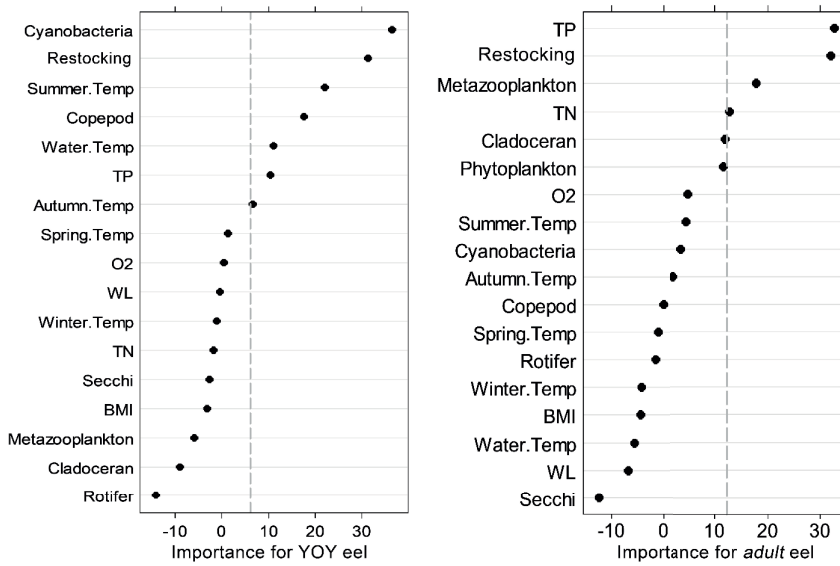

Figure 5. Dot plots of Random Forest model ranking variables for commercial eel catch by importance: A - during the YOY stage (7 years before catch) and B – during the yellow stage (in the year of catch). The right side of the threshold (vertical dashed line) are considered highly important variables for each group, whereas negative and small values are irrelevant for the YOY and yellow eels (**III**).

Cladocera can be among the most important food sources for glass eels in freshwater environments (Belpaire et al., 1992) and is very common also in L. Võrtsjärv (Kangur et al., 2004; Nõges et al., 2004) we theorized that with a negative effect of the rise of cyanobacterial biomass on the cladocerans (Ghadouani et al., 2003; Gliwicz, 1990) it also can affect the restocked glass eels. Besides the influence through food-web relationships, cyanobacterial prevalence can also have other

consequences on the feeding success of larval fish such as lower visibility (making it more difficult to catch the prey; (Utne-Palm, 2002) or clogging of gills (Engström-Öst and Isaksson, 2006).

It was also discovered that copepod biomass in the water body during the year of restocking has a positive effect on the eel yield 7 years later (III, Figures 4, 5), which is surprising as copepods make up only 15% of the total zooplankton abundance in L. Võrtsjärv (Haberman and Haldna, 2014). Copepods serve as intermediate hosts to eel swim bladder parasite *Anguillicola Crassus* (Hubbard et al., 2016; Kirk, 2003), which is known to infect roughly half of the eels inhabiting L. Võrtsjärv (Bernotas and Silm, 2019b). It has been found that the infection with *A. Crassus* can have a positive effect on the growth of eels (Lefebvre et al., 2013). So, we theorized that it could very well be those years when copepod biomass is higher, restocked glass eels also increase their consumption on copepods, which in turn over the eel 7-year growth period results in greater body length and mass for infected individuals but also higher infection ratio in the eel population (**III**).

When we analyzed the factors that could affect the commercial yield of eels during the yellow eel phase at 7 years old, TP and meta zooplankton abundance were the most important factors, which both had a positive effect (Figures 4 & 5, **III**). The exact reason for the TP/meta zooplankton and eel relationship was difficult to interpret, however. Increased movement of eels may play an important role in the higher chance of getting caught during years with high TP concentration or meta zooplankton abundance (**III**).

Do the restocked eels show a clear migration pattern while moving from freshwater to saline environment?

Eight specimens of the tagged 38 eels showed previously undescribed behavior after migrating from freshwater to the sea (Figure 6, **IV**). Instead of swimming towards the ocean, 21% of the tagged eels returned to the river after spending a period in the Baltic Sea only to return to the sea again (**IV**).

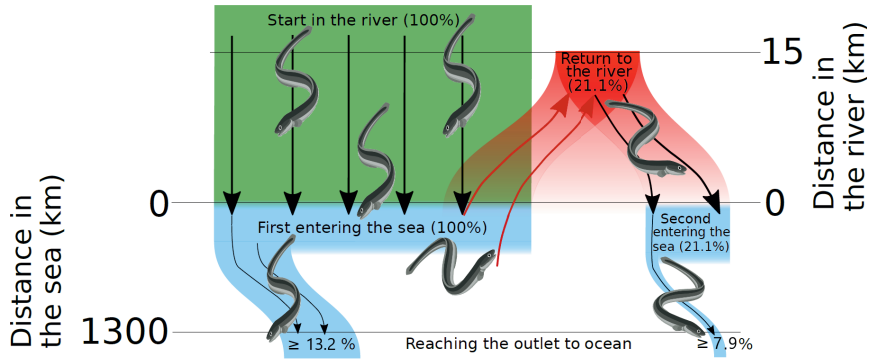

Figure 6. Migration patterns of telemetrically tagged silver European eels. Arrows on green background indicate fish (N = 38) first descending from the Narva River to the Baltic Sea, arrows on red ascending back to the Narva River with the second movement to the sea, arrows on blue migration in the sea to the Danish Straits (outlet to the ocean, **IV**).

The results of our study demonstrated that in total 21% of the tagged eels (N=8 out of 38) that moved from River Narva to the Baltic Sea were detected in the Danish straits on the outlet of the Baltic Sea and three of these eels belonged to the group which indicated the aforementioned unexpected behavior. These 3 eels reached the Danish Straits 68-199 days later from the second descent to the sea. The other 5 specimens that did not return to the river covered the same distance in 314 days on average which indicates adjusting the timing of the migration. There have been numerous publications on the subject of whether restocked Baltic eels are able to migrate (Limburg et al., 2003; Westerberg et al., 2014) or not (Westin, 2003, 1998). Our results show that even some of these (N = 3) specimens that show unconditional migration patterns at first can eventually undertake one of the longest journeys among the restocked eels in the Baltic area to reach the Danish Straits. It also has to be kept in mind that these returning specimens can mix up the estimation of silver eel escapement in places where direct counting or fishing for the migrating silver eels is used. Additionally, these returning eels can be more exposed to local fisheries and predation.

CONCLUSIONS

Our study concentrated on investigating the factors that have affected Estonian eel populations in coastal and freshwaters. Long time series on commercial landings, scientific sampling, restocking, and environmental variables were used to explain the changes in the dynamics of the eel populations. Acoustic telemetry was used for studying the migration patterns of restocked eels.

The decline of commercial and recreational landings since the 1970s in the Estonian coastal eel fishery has been in accordance with the overall drop observed also in other European countries. The reduction of licenses for eel specialized fishing gear such as small fyke nets set in line also played a part in the reduced landings of Estonian coastal eel fisheries however after the Soviet regime collapsed, most of the eels were caught by large fykes and eel is being regarded as a by-catch, meaning it is not specially targeted by the fishery. The number of large fyke net licenses issued for the commercial fishermen has remained largely the same during the last 20 years so the decline in landings can also reflect the declining of the stock. This is confirmed by the monitoring using small fyke nets where the decline in CPUE has followed the trend of the fisheries landings. As the number of eels caught has been low compared to the 1960s and even 1990s fishermen who own licenses for small fyke nets very often do not use the gear at all due to low profitability and heavy workload involved with such type of fishing. However, they still buy the licenses as otherwise, they would lose their historic rights for the license.

Eel restocking is a management measure in many European countries including Estonia. Originally the purpose of restocking of eel in the inland lakes of Estonia served to preserve a traditional eel fishery. With the decline of the eel stock and the implementation of the Eel Management Plan attention was also drawn to the efficiency of the restocking program and the escapement of these restocked eels. The conditions for achieving the best growth conditions were studied among the different water bodies in the restocking program. Restocked eels perform better in lakes with lower restocking densities, well-mixed water column, and rich availability of benthic macroinvertebrates while being restocked as glass eels as opposed to elvers. Also, the prevalence of

cyanobacteria during the year of restocking can have a strong negative impact on the restocked eel population.

Restocked eels are able to migrate from their freshwater habitats to saline waters. However, it might not be as straightforward as mostly thought. A part of the eels that descend to the sea return to the river of departure and can spend prolonged periods in the freshwater before resuming the migration towards the Atlantic Ocean. Although this behavior can increase the vulnerability of these eels to local fisheries and predators it also shows that eels apply different migration strategies that need to be studied further.

Based on the results of this thesis, the following conclusions can be drawn:

- While the decline of commercial eel landings in the coastal sea has been similar to other European countries, the temporary rise in landings at the end of the 1990s and beginning of the 2000s was related to the increase in registering catches, fishing pressure, and quality of fishing gear. Since 2008 the landings of small fyke nets in particular dropped sharply with the main reason being reduced effort as well as the diminishing profitability of using such gear. As opposed to small fyke nets, the number of large fyke net licenses remained unchanged. As eels are not specially targeted by large fykes the changes in the eel landings also reflect the decline of eel biomass in the coastal areas.

- In the inland waterbodies, eels inhabiting L. Võrtsjärv showed faster growth rates and higher Fulton K values compared to specimens populating the small lakes in Narva RBD. In the case of Estonian lakes, the stratified water bodies should be avoided for restocking of eels completely. Well, mixed eutrophic lakes, rich in abundance of Chironomus spp. larvae would be best suited for restocking eels in terms of growth rates, however, the restocking densities should be kept low to prevent unnecessary stress deriving from increased food competition and spreading of diseases.

- Prevalence of cyanobacteria at the time of restocking has the strongest negative impact on the eel landings in the yellow eel

phase in L. Võrtsjärv while copepod biomass in the water body during the year of restocking has the strongest positive impact.

- Silver eels of restocked origin (L. Võrtsjärv) are able to migrate from freshwater to saline environment but may return to freshwaters for prolonged periods. However, these returned specimens are able to resume their migration when conditions become suitable.

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REFERENCES

Baisez, A., Laffaille, P., 2008. Strategy of recreational anglers and estimated eel (Anguilla anguilla) catches in a large European catchment basin, the Loire (France). Knowl Manag Aquat Ecosyst 390–391. https://doi.org/10.1051/kmae/2009002

Belpaire, C., Hodson, P., Pierron, F., Freese, M., 2019. Impact of chemical pollution on Atlantic eels: Facts, research needs, and implications for management. Curr Opin Environ Sci Health. https://doi.org/10.1016/j.coesh.2019.06.008

Belpaire, C., Van Driessche, H., Gao, F.Y., Ollevier, F., 1992. Food and feeding activity of glass eel Anguilla anguilla (L.) stocked in earthen ponds. Irish Fisheries Investigations. Serie A: Freshwater 36, 43–54.

Bernotas, P., Silm, M., 2019a. Report on the eel stock, fishery and other impacts, in Estonia., ICES Scientific Reports. https://doi.org/https://doi.org/10.17895/ices.pub.5545

Bernotas, P., Silm, M., 2019b. Report on the eel stock, fishery and other impacts, in Estonia., ICES Scientific Reports. https://doi.org/https://doi.org/10.17895/ices.pub.5545.

Bernotas, P., Silm, M., Järvalt, A., 2019. Report on the eel stock, fishery and other impacts. Estonia., Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL)., p. 177pp.

Bernotas, P., Vetemaa, M., Saks, L., Eschbaum, R., Verliin, A., Järvalt, A., 2016. Dynamics of European eel landings and stocks in the coastal waters of Estonia. ICES Journal of Marine Science: Journal du Conseil 73, 84–90. https://doi.org/10.1093/icesjms/fsv245

Bisgaard, J., Pedersen, M.I., 1991. Mortality and growth of wild and introduced cultured eels (Anguilla anguilla (L)) in a Danish stream, with special reference to a new tagging technique 9, 57–69.

Bonhommeau, S., Chassot, E., Rivot, E., 2008. Fluctuations in European eel (Anguilla anguilla) recruitment resulting from environmental changes in the Sargasso Sea. Fish Oceanogr 17, 32–44. https://doi.org/10.1111/j.1365-2419.2007.00453.x

Briand, C., Bonhommeau, S., Beaulaton, L., Castelnaud, G., 2007. An appraisal of historical glass eel fisheries and markets: landings,

trade routes and future prospect for management, in: The Institute of Fisheries Management Annual Conference.

Castonguay, M., Hodson, P., Moriarty, C., Drinkwater, K.F., Jessop, B.M., 1994. Is there a role of ocean environment in American and European eel decline? Fish Oceanogr 3, 197–203. https://doi.org/10.1111/j.1365-2419.1994.tb00097.x

De Leo, G.A., Gatto, M., 1996. Trends in vital rates of the European eel: evidence for density dependence? Ecological Applications 6, 1281–1294.

Dekker, W., 2003. Did lack of spawners cause the collapse of the European eel , Anguilla anguilla ? Fisheries Management 365–376.

Durif, C.M.F., Gjøsæter, J., Vøllestad, L.A., 2011. Influence of oceanic factors on Anguilla anguilla (L.) over the twentieth century in coastal habitats of the Skagerrak, southern Norway. Proceedings of the Royal Society B: Biological Sciences 278, 464–473. https://doi.org/10.1098/rspb.2010.1547

Edeline, E., Dufour, S., Elie, P., 2005. Role of glass eel salinity preference in the control of habitat selection and growth plasticity in Anguilla anguilla. Mar Ecol Prog Ser 304, 191–199. https://doi.org/10.3354/meps304191

Engström-Öst, J., Isaksson, I., 2006. Effects of macroalgal exudates and oxygen deficiency on survival and behaviour of fish larvae. J Exp Mar Biol Ecol 335, 227–234. https://doi.org/10.1016/j.jembe.2006.03.007

Engström-Öst, J., Karjalainen, M., Viitasalo, M., 2006. Feeding and refuge use by small fish in the presence of cyanobacteria blooms. Environ Biol Fishes 76, 109–117. https://doi.org/10.1007/s10641-006-9013-8

EU, 2020a. Evaluation of the Eel Regulation, Final Report. https://doi.org/https://doi.org/10.2771/679816

EU, 2020b. Evaluation of the Eel Regulation, Final Report. https://doi.org/https://doi.org/10.2771/679816

European Council, 2007. Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. Official Journal of the European Union 248, 17–23.

Farrell, A.P., Richards, J.G., 2009. Defining Hypoxia: An Integrative Synthesis of the Responses of Fish to Hypoxia, 1st ed, Fish Physiology. Elsevier Inc. https://doi.org/10.1016/S1546-5098(08)00011-3

Feršel, A.-L., Tuvi, E.-L., 2010. Narva jõgi. Hoiualadega jõed Virumaal 2. Keskkonnaamet.

Friedland, K.D., Miller, M.J., Knights, B., 2007. Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. ICES Journal of Marine Science 64, 519–530. https://doi.org/10.1093/icesjms/fsm022

Geeraerts, C., Belpaire, C., 2010. The effects of contaminants in European eel: A review. Ecotoxicology 19, 239–266. https://doi.org/10.1007/s10646-009-0424-0

Geeraerts, C., Focant, J.F., Eppe, G., De Pauw, E., Belpaire, C., 2011. Reproduction of European eel jeopardised by high levels of dioxins and dioxin-like PCBs? Science of the Total Environment 409, 4039–4047. https://doi.org/10.1016/j.scitotenv.2011.05.046

Ghadouani, A., Pinel-Alloul, B., Prepas, E.E., 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. Freshw Biol 48, 363–381. https://doi.org/10.1046/j.1365-2427.2003.01010.x

Gliwicz, Z.M., 1990. Why do cladocerans fail to control algal blooms? Hydrobiologia 200–201, 83–97. https://doi.org/10.1007/BF02530331

Haberman, J., Haldna, M., 2014. Indices of zooplankton community as valuable tools in assessing the trophic state and water quality of eutrophic lakes: Long term study of Lake Võrtsjärv. J Limnol 73, 61–71. https://doi.org/10.4081/jlimnol.2014.828

Hanel, R., Brand, C., Diaz, E., Döring, R., Sapounidis, A., Warmerdam, W., Andres, M., Freese, M., Marcelis, M., Marohn, L., Pohlmann, J., van Scharrenburg, M., Waidmann, N., Walstra, J., Werkman, M., DeWilde, J., Wysujack, K., 2019. Research for PECH Committee-Environmental , social and economic sustainability of European eel management 192.

Hanel, R., Stepputtis, D., Bonhommeau, S., Castonguay, M., Schaber, M., Wysujack, K., Vobach, M., Miller, M.J., 2014. Low larval abundance in the Sargasso Sea: new evidence about reduced

recruitment of the Atlantic eels. Naturwissenschaften 101, 1041–1054. https://doi.org/10.1007/s00114-014-1243-6

Heinis, F., Davids, C., 1993. Factors governing the spatial and temporal distribution of chironomid larvae in the Maarsseveen lakes with special emphasis on the role of oxygen conditions. Netherland Journal of Aquatic Ecology 27, 21–34.

HELCOM, 1996. Third periodic assessment of the state of the marine enviroment of the Baltic Sea, 1989-1993, Background document, Baltic Sea Environ.Proc. Helsinki Commission, Baltic Marine Environment Protection Commission.

Hubbard, I.M., Hill-Spanik, K.M., Knott, D., Buron, I. de, 2016. Development of Anguillicoloides crassus in a Cyclopoid Copepod from the Acanthocyclops robustus–americanus–vernalis Complex in South Carolina, U.S.A. . Comp Parasitol 83, 192–196. https://doi.org/10.1654/4835sed.1

Huntingford, F.A., Adams, C., Braithwaite, V.A., Kadri, S., Pottinger, T.G., Sandøe, P., Turnbull, J.F., 2006. Current issues in fish welfare. J Fish Biol 68, 332–372. https://doi.org/10.1111/j.0022-1112.2006.001046.x

ICES, 2020a. Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL). ICES Scientific Reports 2, 223. https://doi.org/http://doi.org/10.17895/ices.pub.5982

ICES, 2020b. European eel (Anguilla anguilla) throughout its natural range. ICES Advice on fishing opportunities, catch, and effort 1–5.

ICES, 2020c. Working Group on Recreational Fisheries Surveys (WGRFS; outputs from 2019 meeting). ICES Scientific Reports 2, 78. https://doi.org/http://doi.org/10.17895/ices.pub.5744

ICES, 2019. JOINT EIFAAC/ICES/GFCM WORKING GROUP ON EELS (WGEEL). Country Reports 2018-2019: Eel stock, fisheries and habitat reported by country 483.

ICES, 2010. EIFAC / ICES WGEEL REPORT 2010 ACOM EIFAC / ICES Working Group on Eels (WGEEL) Report of the 2010 session of the Joint. https://doi.org/ICES CM 2015/ACOM:18

ICES, 2006. Report of the 2006 session of the Joint EIFAC / ICES Working Group on Eels Report of the 2006 Session of the Joint

EIFAC / ICES Working Group on Eels. Fisheries Management 1–214.

ICES, 1977. ICES Statistical Rectangle Coding System. ICES Document CM 1977/Gen: 3.

Janatian, N., Olli, K., Cremona, F., Laas, A., Nõges, P., 2020. Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake. Limnol Oceanogr 65, 717–731. https://doi.org/10.1002/lno.11342

Järvalt, A., 2008. Eel Management Plan Estonia 2008. Ministry of Environment 26.

Järvalt, A., 2003. Fishes and fishery of L. Võrtsjärv. Lake Võrtsjärv 335–354.

Järvet, A., 2004. Hydrology of Lake Võrtsjärv. Lake Võrtsjärv 105–139.

Kangur, A., 1998. European Eel, Anguilla anguilla(L.) Fishery in Lake Vortsjaerv: Current Status and Stock Enhancement Measures. Limnologica 28, 95–101.

Kangur, A., Kangur, P., Kangur, K., Järvalt, A., Haldna, M., 2010. Anguillicoloides crassus infection of European eel, Anguilla anguilla (L.), in inland waters of Estonia: History of introduction, prevalence and intensity. Journal of Applied Ichthyology 26, 74–80. https://doi.org/10.1111/j.1439-0426.2010.01497.x

Kangur, K., Kangur, A., Kangur, P., 1999. A comparative study on the feeding of eel, Anguilla anguilla (L.), bream, Abramis brama (L.) and ruffe, Gymnocephalus cernuus (L.) in Lake Võrtsjärv, Estonia, in: Shallow Lakes' 98. Springer, pp. 65–72.

Kangur, K., Timm, H., Timm, T., 2004. Zoobenthos. Lake Võrtsjärv 265–280.

Kangur, K., Timm, H., Timm, T., Timm, V., 1998. Long-term changes in the macrozoobenthos of Lake Võrtsjärv. Limnologica 28, 75–83.

Karjalainen, M., Engström-Öst, J., Korpinen, S., Peltonen, H., Pääkkönen, J.P., Rönkkönen, S., Suikkanen, S., Viitasalo, M., 2007. Ecosystem consequences of cyanobacteria in the northern Baltic Sea. Ambio 36, 195–202. https://doi.org/10.1579/0044-7447(2007)36[195:ECOCIT]2.0.CO;2

Kint, P., 1940. Kalandus 1939. Eesti kalandus 4, 85–102.

Kirk, R.S., 2003. The impact of Anguillicola crassus on European eels. Fish Manag Ecol 10, 385–394. https://doi.org/10.1111/j.1365-2400.2003.00355.x

Knights, B., 2003. A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere. Science of the Total Environment 310, 237–244. https://doi.org/10.1016/S0048-9697(02)00644-7

Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K., Ojaveer, H., 2008. Gulf of Riga and Pärnu Bay, in: Schiewer, U. (Ed.), Ecology of Baltic Coastal Waters. Springer, Berlin, pp. 217–239.

Lafferty, K.D., Holt, R.D., 2003. How should environmental stress affect the population dynamics of disease? Ecol Lett 6, 654–664. https://doi.org/10.1046/j.1461-0248.2003.00480.x

Lefebvre, F., Fazio, G., Mounaix, B., Crivelli, A.J., 2013. Is the continental life of the European eel Anguilla anguilla affected by the parasitic invader Anguillicoloides crassus? Proceedings of the Royal Society B: Biological Sciences 280. https://doi.org/10.1098/rspb.2012.2916

Limburg, K.E., Wickstrom, H., Svedang, H., Elfman, M., Kristiansson, P., 2003. Do stocked freshwater eels migrate? Evidence from the Baltic suggests "yes." Biology, Management, and Protection of Catadromous Eels 33, 275–284. https://doi.org/migration microchimie otolithe Sr/Ca anguille argentee

Lin, Y.-J., Ložys, L., Shiao, J.-C., Iizuka, Y., Tzeng, W.-N., 2007. Growth differences between naturally recruited and stocked European eel Anguilla anguilla from different habitats in Lithuania. J Fish Biol 71, 1773–1787. https://doi.org/10.1111/j.1095-8649.2007.01642.x

McKenzie, D.J., Piccolella, M., Dalla Valle, A.Z., Taylor, E.W., Bolis, C.L., Steffensen, J.F., 2003. Tolerance of chronic hypercapnia by the European eel Anguilla anguilla. Journal of Experimental Biology 206, 1717–1726. https://doi.org/10.1242/jeb.00352

Molnár, K., Baska, F., Csaba, G., Glávits, R., Székely, C., 1993. Pathological and histopatnotogical studies of the swimbladder of eels Anguilla anguitla infected by Angutlticpta crassus (Nemafoda: Dracuncuioidea). Dis Aquat Organ 15, 41–50.

Mouton, A.M., Stevens, M., Den Neucker, T. Van, Buysse, D., Coeck, J., 2011. Adjusted barrier management to improve glass eel migration at an estuarine barrier. Mar Ecol Prog Ser 439, 213–222. https://doi.org/10.3354/meps09325

Nõges, P., Laugaste, R., Nõges, T., 2004. Phytolankton, in: Haberman, J., Pihu, E. (Eds.), Lake Vortsjärv. Estonian Encyclopaedia Publishers, Tallinn. Estonian Encyclopaedia Publishers, Tallinn, pp. 217–231.

Nõges, P., Nõges, T., 2014. Weak trends in ice phenology of Estonian large lakes despite significant warming trends. Hydrobiologia 731, 5–18. https://doi.org/10.1007/s10750-013-1572-z

Nõges, T., Anneville, O., Guillard, J., Haberman, J., Järvalt, A., Manca, M., Morabito, G., Rogora, M., Thackeray, S.J., Volta, P., Winfield, I.J., Nõges, P., 2018. Fisheries impacts on lake ecosystem structure in the context of a changing climate and trophic state. J Limnol 77, 46–61. https://doi.org/10.4081/jlimnol.2017.1640

Nõges, T., Arst, H., Laas, A., Kauer, T., Nõges, P., Toming, K., 2011. Reconstructed long-term time series of phytoplankton primary production of a large shallow temperate lake: The basis to assess the carbon balance and its climate sensitivity. Hydrobiologia 667, 205–222. https://doi.org/10.1007/s10750-011-0647-y

Orav-Kotta, H., Kotta, J., Kotta, I., 2004. Comparison of macrozoobenthic communities between the 1960s and the 1990s – 2000s in the Väinameri , NE Baltic Sea 283–291.

Ott, I., 2016a. Eesti väikejärvede hüdrobioloogiline seire. 2016. Eesti siseveekogude seire alamprogramm. Tartu.

Ott, I., 2016b. Eesti väikejärvede hüdrobioloogiline seire. 2016. Eesti siseveekogude seire alamprogramm. Tartu.

Pedersen, M.I., Jepsen, N., Rasmussen, G., 2017. Survival and growth compared between wild and farmed eel stocked in freshwater ponds. Fish Res 194, 112–116. https://doi.org/10.1016/j.fishres.2017.05.013

Perry, S.F., Reid, S.D., 1992. Relationship between blood O2 content and catecholamine levels during hypoxia in rainbow trout and American eel. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 263, R240--R249.

Pihu, E., 1998. Fishes and fisheries management in Lake Võrtsjärv. Limnologica 28, 91–94.

Piirsoo, K., Pall, P., Tuvikene, A., Viik, M., Vilbaste, S., 2010. Narva jõe veekvaliteedi hindamine Ungaris väljatöötatud potamoplanktilise meetodi abil. Estonian Journal of Ecology 59, 243–258. https://doi.org/10.3176/eco.2010.4.01

Pitkänen, H., Lehtoranta, J., Peltonen, H., 2008. The Gulf of Finland, in: Schiewer, U. (Ed.), Ecology of Baltic Coastal Waters. . Springer, Berlin, pp. 285–304.

Poole, W.R., Reynolds, J.D., 1996. Growth rate and age at migration of Anguilla anguilla. J Fish Biol 48, 633–642.

Shiao, J.C., Ložys, L., Iizuka, Y., Tzeng, W.N., 2006. Migratory patterns and contribution of stocking to the population of European eel in Lithuanian waters as indicated by otolith Sr:Ca ratios. J Fish Biol 69, 749–769. https://doi.org/10.1111/j.1095-8649.2006.01147.x

Simon, J., 2007. Age, growth, and condition of European eel (Anguilla anguilla) from six lakes in the River Havel system (Germany). ICES Journal of Marine Science 64, 1414–1422. https://doi.org/10.1093/icesjms/fsm093

Simon, J., Dörner, H., 2014. Survival and growth of European eels stocked as glass- and farm-sourced eels in five lakes in the first years after stocking. Ecol Freshw Fish 23, 40–48. https://doi.org/10.1111/eff.12050

Simon, J., Dörner, H., Scott, R.D., Schreckenbach, K., Knösche, R., 2013. Comparison of growth and condition of European eels stocked as glass and farm sourced eels in lakes in the first 4 years after stocking. Journal of Applied Ichthyology 29, 323–330. https://doi.org/10.1111/jai.12078

Suursaar, Ü., Kullas, T., Otsmann, M., 2001. THE INFLUENCE OF CURRENTS AND WAVES ON ECOLOGICAL CONDITIONS 231–247.

Teesalu, P., 2019. The Role of trophic niche in eel head shape dimorphism. Eesti Maaülikool.

Tesch, F.W., Bartsch, P., Berg, R., Gabriel, O., Henderson, I.W., Kamstra, A., Kloppmann, M., Reimer, L.W., Wirth, T., White, R.J., Thorpe, J.E., 2003. The Eel.

Tõnno, I., Agasild, H., Kõiv, T., Freiberg, R., Nõges, P., Nõges, T., 2016. Algal diet of small-bodied crustacean zooplankton in a cyanobacteria-dominated eutrophic lake. PLoS One 11, 1–17. https://doi.org/10.1371/journal.pone.0154526

Tuvikene, L., Nõges, T., Nõges, P., 2011. Why do phytoplankton species composition and "traditional" water quality parameters indicate different ecological status of a large shallow lake? Hydrobiologia 660, 3–15. https://doi.org/10.1007/s10750-010-0414-5

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. Mar Freshw Behav Physiol 35, 111–128. https://doi.org/10.1080/10236240290025644

Vasilyev, P.A., 1974. The main preconditions for organization of commercial fishing of the eel in Narva River. Izvestija GOSNIORH 83, 144–152.

Vetemaa, M., Eschbaum, R., Saat, T., 2006. The transition from the Soviet system to a market economy as a cause of instability in the Estonian coastal fisheries sector. Mar Policy 30, 635–640. https://doi.org/10.1016/j.marpol.2005.08.001

Westerberg, H., Sjöberg, N., Lagenfelt, I., Aarestrup, K., Righton, D., 2014. Behaviour of stocked and naturally recruited European eels during migration. Mar Ecol Prog Ser 496, 145–157. https://doi.org/10.3354/meps10646

Westin, L., 2003. Migration failure in stocked eels Anguilla anguilla. Mar Ecol Prog Ser 254, 307–311. https://doi.org/10.3354/meps254307

Westin, L., 1998. The spawning migration of European silver eel (Anguilla anguilla L.) with particular reference to stocked eel in the Baltic. Fish Res 38, 257–270. https://doi.org/10.1016/S0165-7836(98)00162-3

White, E.M., Knights, B., 1997. Dynamics of upstream migration of the European eel, Anguilla anguilla (L.), in the Rivers Severn and Avon, England, with special reference to the effects of man-made barriers. Fish Manag Ecol 4, 311–324. https://doi.org/10.1046/j.1365-2400.1997.00050.x

Wielgoss, S., Taraschewski, H., Meyer, A., Wirth, T., 2008. Population structure of the parasitic nematode Anguillicola crassus, an invader

of declining North Atlantic eel stocks. Mol Ecol 17, 3478–3495. https://doi.org/10.1111/j.1365-294X.2008.03855.x

Würtz, J., Taraschewski, H., Pelster, B., 1996. Changes in gas composition in the swimbladder of the European eel (Anguilla anguilla) infected with Anguillicola crassus (Nematoda). Parasitology 112, 233–238. https://doi.org/10.1017/s003118200008481x

SUMMARY IN ESTONIAN

Meie uuring keskendus Eesti ranniku- ja magevee angerja populatsioone mõjutanud tegurite uurimisele. Angerjapopulatsioonide dünaamika muutuste selgitamiseks kasutati kutseliste saagiandmete, teaduslike katsepüükide, asustamise ja keskkonnamuutujate pikaajalisi aegridu. Asustatud angerjate rännete uurimiseks kasutati akustilist telemeetriat.

Angerjasaakide langus Eesti rannikumeres alates 1970ndatest on sarnane üle-Euroopalise trendiga. Kuigi 1990ndatel toimus saakide mõningane tõus, võis seda seletada poliitilise režiimi vahetumisega, kalapüügivahendite kvaliteedi- ning andmete esitamise täpsuse paranemisega. Kutseliste kalurite seas läbi viidud küsitlus näitas ka, et 1980ndatel toimus 40% ulatuses angerjasaakide mittetäielik registreerimine. Alates 2008. aastal vastu võetud Eesti Angerjamajandamiskava rakendamisest vähendati angerjapüügiks spetsiifiliste püügivahendite (rivimõrrad) lubade arvu 50% ulatuses, mis vähendas oluliselt ka vastavate püügivahenditega registreeritud saaki. Põhiosa angerjasaagist saadakse kas ääre- või avaveemõrdadega, mille lubade arv on viimase 20 aasta jooksul püsinud stabiilsena. Kuna ääre- või avaveemõrdu kasutatakse rannikumeres peamiselt muude liikide püüdmiseks (ahven, tint, haug, särg jne), võib angerjasaakide muutus peegeldada ka angerjavaru üldist seisu Eesti rannikumeres.

Eesti siseveekogude angerjapopulatsioon põhineb suures osas asustamisel. Põhiosa angerjatest asustatakse Eestis Võrtsjärve, kuid 2000ndate aastate algusest on angerjaid asustatud ka Peipsi vesikonna väikejärvedesse. Asustamise eesmärgiks on olnud traditsioonilise angerjapüügi säilitamine peamiselt Võrtsjärves, kuid seoses Eesti Angerjamajanduskava rakendamisega ka Euroopa Nõukogu regulatsioonist 1100/2007 tulenev 40% hõbeangerja biomassi merre pääsemise nõude täitmine. Kuigi väljarändavate hõbeangerjate biomassi on alates 2016. aastast arvutuslikult hinnatud, on tegelik kogus siiani mõnevõrra ebaselge. Küll aga on võimalik hinnata faktoreid, mis asustatud angerjaid erinevat tüüpi veekogudes mõjutavad. Kui head kasvuparameetrid iseloomustavad kala heaolu, tuleb asustamiseks sobilike veekogude valimisel seda arvestada. Asustatud angerjad kasvavad kiiremini hästi segunevates, rikkaliku põhjaloomastikuga eutroofsetes järvedes, kus asustustihedus on madal ning asustatakse klaasangerja staadiumis olevaid

kalu. Sellest tulenevalt sobib näiteks Võrtsjärv angerjate asutamiseks paremini Vooremaa väikejärvedest. Võrtsjärve näitel on oluline teada, et kõrge sinivetikate arvukus järvevees asustamise aastal mõjub asustatud angerjapopulatsioonile negatiivselt, väljendudes madalamas saagikuses 7 aastat pärast asustamist, mil antud põlvkond kõige rohkearvulisemalt angerjasaagis esineb. See negatiivne mõju võib avalduda läbi järve toiduahela, kus tänu sinivetikate suurele arvule langeb zooplanktoni kvaliteet, mis omakorda on asustatud klaasangerjatele esimeseks toiduks järves. Samas võib sinivetikatel olla ka puhtalt häiriv mõju asustatud angerjatele. Tänu vähenenud vee läbipaistvusele on angerjatel keerulisem saaki kätte saada või ummistavad sinivetikad angerjate lõpuseid, takistades nii gaasivahetust.

Eestis asustatud angerjad on võimelised mageveest merevette rändama. Narva jõe kaudu Läänemerre jõudvad hõbeangerjad näitavad oma rändekäitumises erinevaid mustreid, mida varasemalt ei ole täheldatud. 21% (8 isendit 38st) merre laskunud hõbeangerja puhul kinnitasime rännet Narva jõe suudmest Taani väinadesse. Samas pöördus 21% merre laskunud hõbeangerjatest pärast mitmeid kuid meres viibimist tagasi Narva jõkke, misjärel nad uuesti merre rändasid. Nendest kaladest, kes tagasi jõkke pöördusid jõudis Taani väinadesse omakorda 37% (3 isendit). Need tulemused näitavad, et hõbeangerjad võivad rännet väga erinevalt läbi viia ning vastavalt vajadusele ajastada.

Töö tulemusena leiti järgmist:

- Kuigi angerjasaakide langus rannikumeres on sarnane teiste Euroopa riikidega, oli ajutine tõus 1990. aastate lõpus ja 2000. aastate alguses seotud püügimahu- ja püügikoormuse suurenemisega ning püügivahendite kvaliteedi paranemisega. Alates 2008. aastast vähenesid järsult rivimõrdade saagid, peamiseks põhjuseks oli püügilubade vähendamine ning antud püügivahendi madal kasumlikkus. Isegi püügilube omavad kalurid ei asetanud sageli rivimõrdu tänu madalale saagikusele püügile. Erinevalt rivimõrdadest jäi ääre- ja avaveemõrdade lubade arv muutumatuks. Kuna ääre- ja avaveemõrrad ei ole spetsiaalselt angerjapüügiks kohandatud ning angerjas satub neisse pigem kaaspüügina, peegeldavad muutused angerja saakides ka angerja biomassi langust rannikualadel.

- Võrtsjärves elavad angerjad näitasid kiiremat kasvukiirust ja kõrgemaid Fultoni konditsioonifaktori väärtusi võrreldes Narva Jõe Vesikonna väikejärvedes elavate isenditega. Eesti järvede puhul tuleks angerjate asustamisel vältida kihistunud veekogusid. Angerjate asustamiseks sobivad kõige paremini hästi segunenud eutroofsed järved, milles esineb rikkalikult sääsevastseid. Siiski peaksid asustustihedused olema madalad, et vältida angerjate liigset stressi, mis tuleneb toidukonkurentsi suurenemisest ja haiguste levikust.

- Keskkonnatingimused asustamise hetkel võivad mõjutada angerjapopulatsiooni nii negatiivselt kui positiivselt. Meie tulemused näitasid, et sinivetikate suur arvukus asustamise aastal mõjutab angerjaid negatiivselt kollase angerja faasis (7 aastat pärast asustamist), samas kui aerjalgsete rohkus asustamise aastal avaldab kõige tugevamat positiivset mõju.

- Võrtsjärvest pärit hõbeangerjad suudavad rännata mageveest merevette, kuid võivad pikaks ajaks tagasi magevette naasta. Seejärel on need naasnud angerjad võimelised uuesti kuderändele asuma.

I

ORIGINAL PUBLICATIONS

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Contribution to the Symposium: '*International Eel Symposium 2014*'

Original Article

Dynamics of European eel landings and stocks in the coastal waters of Estonia

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European eel stocks are in a decline all over Europe. In Estonia, we analysed three different dataseries (commercial landings 1969 – 2014, scientific eel monitoring 1998 – 2014, and recreational catches 2005 – 2012). In the commercial fishery, the biggest drop in landings occurred in the 1980s, with a small recovery in the end of the 1990s. We also interviewed fishers to evaluate the quality of the official catch figures. In the monitoring dataseries, gathered by the use of special eel fykenets, the steepest cpue decline occurred in the last 5 years. Finally, recreational eel fishery has almost stopped: in 2012, catches were only 3% of that in 2005. In conclusion, both professional and recreational eel catches have declined in all the coastal areas of Estonia. The number of professional and recreational fishers specialized to eel fishing has decreased and the number of licences for eel-specific fishing gear has been reduced.

Keywords: *Anguilla anguilla*, coastal fishery, eel, Estonia, European eel, population dynamics.

Introduction

European eel stock has been in decline for decades (ICES, 2014) and the eel catches in the Baltic Sea show a steady diminishing rate (ICES, 2013). Several hypotheses have been brought forward to explain this decline: namely loss of habitats, oceanic current changes, overfishing, spreading of parasites, and pollution (Dekker, 2003). Compared with 1960–1979, the current level of recruitment of the continental yellow eel is under 10% (ICES, 2010). All eel fishing countries in the Baltic Sea region currently report the lowest eel landings in history (ICES, 2013). For example, in 2012, Swedish catch made up only 50% of the 2002–2012 average (ICES, 2013). The same happened in Germany, where the 2012 Baltic Sea landings formed 47% of the same period average (ICES, 2013).

European Union has launched a legislative act (Council Regulation No. 1100/2007) establishing measures for the recovery of the stock of European eel. This regulation requires all member states to implement their eel management plans (EMPs). Estonian EMP was put into practice in 2008. The EMPs must include an overview of the status of both stocked and natural eel stock. While stocked populations of eel in Estonia have been studied in detail (Järvalt, 2008; ICES, 2013), the natural populations that inhabit the coastal waters have been far less examined. Considering that the eels residing in the saline and brackish coastal waters might contribute extensively to the spawning stock (ICES, 2009; Simon *et al.*, 2013), it is indispensable to have an overview of the available data.

Historically, eel has been one of the most appreciated species among the Estonian fishers (Pihu and Turovski, 2001). Eel landings were on its peak in Estonian waters before World War II when annual catches surpassed 500 t, with most of the eel caught from the coastal sea (Kint, 1940). While the landings in coastal waters have not been high in recent times (averaging around 7 t year^{-1} in the last 10 years), eel is treasured for its high sale value (first buyer prices averaged 7.41€ per kg in 2014). However, over 90% of the wild eel sold for consumption in Estonia comes from freshwater fisheries that rely almost exclusively on stocking. Unfortunately, it is impossible to compare results with neighbouring Latvia and Russia, since no marine catch data are available from there (ICES, 2013). In Finnish professional marine fishery, the average landings for the last 10 years were 1.22 t annually (ICES, 2014).

Although the regression of the eel stocks in Estonian coastal waters is acknowledged, and also discussed between fishers, there is no overview on this topic in the scientific literature. This study

compiles both professional and recreational fisheries catches and compares it with the scientific monitoring dataseries (started in 1998) from six monitoring areas along the Estonian coast.

Material and methods

Study area

Our study area consists of four main districts: Gulf of Finland (ICES Subdivision 32), Gulf of Riga (ICES Subdivision 28-1), Baltic Proper (ICES Subdivisions 28-2 and 29-2), and Väinameri (ICES Subdivision 29-4; Figure 1).

The Gulf of Finland stretches from the northwestern corner of Estonia to the Neva Bay in Russia covering an area of 29 600 km^2. The mean depth of the gulf is 38 m (HELCOM, 1996). The trophic level ranges from mesotrophic in the western part to eutrophic in the eastern part of the gulf (Pitkänen *et al.*, 2008). It has the highest freshwater inflow in the Baltic Sea, relative to its surface area, yet the overall oxygen conditions in the gulf are poor. This is mainly due to spring algal blooms and the sedimentation of detrital plankton material, which derive directly from high winter nutrient concentrations (Pitkänen *et al.*, 2008).

The Gulf of Riga has a surface area of 16 330 km^2 and is adjoined by Estonia and Latvia (Kotta *et al.*, 2008). It is directly connected to the Baltic proper and Väinameri. The gulf is fairly shallow with the mean depth being 27 m, and due to strong vertical mixing of the water column, the oxygen regime is relatively good. The turbulence and vertical mixing has its effect on water transparency making it rather low. The benthos-related invertebrate and fish species have formed substantial populations in the gulf (Kotta *et al.*, 2008).

Väinameri (also known as The Sea of Straits or West Estonian Archipelago Sea) is shallow semi-enclosed area between the islands of Saaremaa, Hiiumaa, and Muhumaa, and the western coast of Estonian mainland. It is the smallest of the study areas with a surface area of 2243 km^2. Väinameri is very shallow with depths from 3 to 8 m prevailing (Suursaar *et al.*, 2001). Despite its small surface area, Väinameri has a large quantity of different biotopes and a rich benthic diversity (Orav-Kotta *et al.*, 2004).

The Baltic proper fisheries concern the southwestern, northwestern, and western coasts of the islands Hiiumaa and Saaremaa.

Figure 1. The four different districts of the study field. The numbers mark Estonian Marine Institute monitoring areas: 1—Saarnaki, 2—Kihnu, 3—Kõiguste, 4—Käsmu, 5—Matsalu, and 6—Vilsandi.

Estonia is divided into two river basin districts (RBD), according to the EMP (Järvalt, 2008). The Narva RBD consists of freshwater fisheries that rely entirely on stocking. The natural eel population of Estonia resides in the West Estonian RBD.

Fisheries

There has never been a yellow- or silver eel-specific fishery in Estonia, and all fisheries are oriented towards both. However, size limits apply for the catch. The lowest legal size of the eels caught in the coastal sea is total length (TL) = 35 cm and for inland waterbodies (excluding L. Võrtsjärv, L. Peipus, and L. Pskov where the limit is 55 cm) the size limit is TL = 50 cm.

Professional eel fishing gear in Estonian coastal waters mainly consists of different sized fykenets (mouth sizes up to 3 m) and smaller fykenets set in line. It has to be mentioned that in large fykenets (mouth >3 m), eel is mostly regarded as side-catch (1% of total catch) and thus not significant (Järvalt, 2008). That is the reason this kind of gear cannot be counted as specialized eel fishing gear. Fishers who specialize in eel fishing use mainly special smaller fykenets (typically set in line) or longlines. The amount of small fykenets licences in active fishing has been reduced by 50% over the period 2009–2014. Long-lining is professionally carried out only in very small extent (1.7 kg of eel reported in 2014). However, recreational fishers use longlines with 100 hooks per line as the main gear for eel fishing. Up to 100 hooks (300 hooks for recreational fishers residing on small islands with permanent settlement) per line and one line per recreational fisher are allowed by the Estonian Fishing Law (https://www.riigiteataja.ee/en/eli/503092014004/consolide).

In 2013, there were 1086 licenced fishers or companies operating in the Estonian coastal fisheries. One hundred and thirty-eight of them reported eel catches, with only three reporting >50 kg in total.

Data sources

Three main data sources were used in this study. First, the catch registered by professional fishers. These include information on the date, gear type, fished species, and weight (kg) of the catch by the ICES Subdivision and statistical rectangles (ICES, 1977). These records are collected by the Ministry of Agriculture monthly and are available in electronic form from 2008 onwards. Most data-deficient periods are the late 1980s and early 1990s as some records are missing from that interval and overall reliability of the data from that period is questionable. The database obtained from the Ministry of Agriculture contained entries for eel catches over the period 2008–2014. Each record featured information on the catch area (ICES—subdivision and statistical rectangle), county of report, type of gear, harbour, month, and the size of catch. The database in conjunction with records from different publications (Aps, 1996; Vetemaa *et al.*, 2002; Vetemaa and Eero, 2005) was combined into one to characterize the changes in the eel catches over the last 45 years. The catch data concerning the soviet period (1969–1991) were obtained from the databases of Estonian Marine Institute. The second source used in the study was the recreational fishing database operated by the Ministry of Environment (https://kala.envir.ee/). This comprised data on all the recreationally fished Estonian waters and has entries dating back to 2008. The information includes fishing date and gear, fished species, and volume of the catch (kg). In the present study, the cpue was calculated and fishing effort (100 hooks a night) was separated from the data.

The third source is the data collected by the Estonian Marine Institute. Small fykenets were used for annual coastal eel

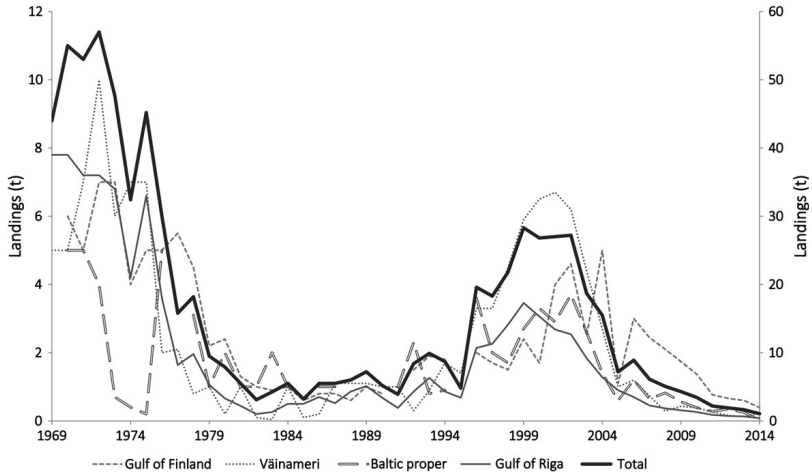

Figure 2. Total landings of eel (in tonnes) in 1969–2014. The "Gulf of Riga" and "Total" graphs correspond to the scale on the right.

monitoring. The gear is 55 cm high with a semi-circular opening and a leader or wing that is 5 m long. Fykes are made of 17-mm mesh in the arm and 10-mm in the codend with yarn quality no 201/12 in twisted nylon. Most yellow eel were caught using this gear. The average fishing effort for each area/year was 161 fyke days (1 d = 24 h soaking time). Catch per unit effort (cpue) data are presented as an average number of eels caught per fyke/day by study years and monitoring areas.

Questionnaire

As there were inconsistencies in the professional fishery data concerning the end of the soviet era, a telephone interview was made with coastal fishers who were actively fishing in the 1980s to evaluate if rumours from this time (e.g. that large amounts of eel were used as exchange for goods or services, and that the official eel catches from this time are great underestimation) have real ground. Chosen fishers were questioned about the credibility of the historical landings, the preference in eel fishing gear, and whether they had used it in the last 5 years. The fishers were chosen from all Estonian coastal areas and from the oldest age group (fishers born from 1945 to 1955, i.e. those who worked already at least 30 years ago). There were 97 individuals matching the criteria from whom 50 were randomly selected for the survey.

Results

The commercial eel catches show a moderate negative correlation between total landings and studied year for the period 1969–2014 (Spearman's correlation, $r_s = -0.52$, $n = 46$, $p < 0.001$). In the Soviet period (1969–1991), the negative correlation was very strong ($r_s = -0.84$, $n = 23$, $p < 0.001$) as the official landings dropped from 57 t in 1972 to 3.9 t in 1991. The Estonian period (1992–2014) also showed a strong negative correlation between total landings and year ($r_s = -0.63$, $n = 23$, $p = 0.001$), regardless of the increase in the landings at the beginning of the period (Figure 2). This decline was also significant in all studied areas separately: Gulf of Finland ($r_s = -0.44$, $n = 43$, $p = 0.002$), Gulf of Riga ($r_s = -0.55$, $n = 46$, $p < 0.001$), Väinameri ($r_s = -0.34$, $n = 46$, $p = 0.02$), Baltic proper ($r_s = -0.44$, $n = 39$, $p = 0.004$).

The reported recreational eel catches for the period 2005–2012 also showed significant decline ($r_s = -0.9$, $n = 8$, $p < 0.001$). The decline was also significant if all research areas were considered separately (Figure 3).

In total, 194 separate catch data points were found in the Recreational Fisheries Database. The results do not show a significant decrease in the cpue of the longlines ($r_s = -0.2$, $n = 5$, $p = 0.7$). However, fishing effort decreased significantly ($r_s = -0.9$, $n = 5$, $p = 0.03$; Figure 4).

A total of 407 eels were caught with an average total length of 58 cm and a mean weight of 413 g in the monitoring catches by Estonian Marine Institute during 1998–2013. The currently ongoing monitoring started as follows: Saarnaki—1998, Kihnu—1998, Kõiguste—2006, Käsmu—1999, Matsalu—2000, and Vilsandi—1998. The decline in cpue (specimens per fyke day) values (Figure 5) for all research areas was statistically significant ($r_s = -0.41$, $n = 85$, $p < 0.001$).

The number of small fykenet licenses allowed by the Minister of Environment in the Estonian coastal fisheries was reduced from 4830 in 2008 to 2414 in 2014. The decrease in small fykenets total catch has been notable ($r_s = 0.9$, $n = 7$, $p < 0.001$, Table 1).

The questionnaire of coastal fishers ($n = 50$) revealed that 60% ($s = 30.9$) of the eels caught were officially reported in the period 1980–1992. An average coastal fisher in the studied sample had been working in this field for 39.3 years ($s = 10.1$ years). There has been a significant change in gear use by professional fishers

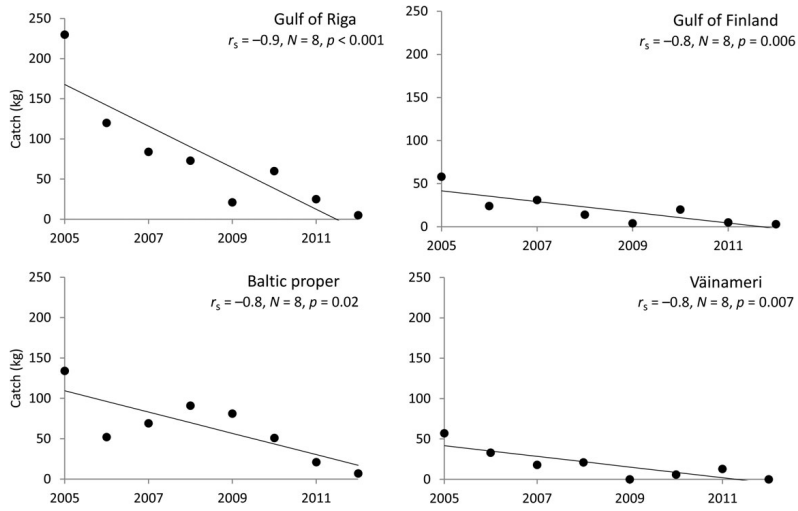

Figure 3. The decline of recreational eel catches volume in 2005–2012.

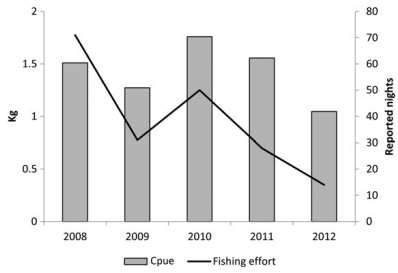

Figure 4. Cpue [kg (100 hooks)$^{-1}$] of longlines for Estonian coastal sea compared with the fishing effort according to the recreational fishing database. Cpue corresponds to the scale on the left.

($\chi^2 = 34.6$, d.f. = 3, $p < 0.0001$) comparing data from periods 1980–1992 (results of the fishers questionnaire) and 2006–2013 (results from official database; Figure 6). About 70% ($n = 35$) of the coastal fishers questioned in the survey told that they have not used small fykenets in the last 5 years due to the unprofitability of this type of fishing.

Discussion

The decline of eel catches during the last half century has been noticed in all Estonian coastal areas. The starting point of the decline (early 1970s) coincides roughly with the rest of Europe, and has, with some improvements in the end of 1990s, continued to present day (Figure 2). In 2014, reported eel catches from coastal fishers in the Gulf of Riga were 0.4 t in total, while, for example, in 2004 it was 6.4 t—this corresponds to a 94% decrease over the last 10 years. A similar trend can be observed for the total Estonian coastal catch—landings in 2014 made only 6.7% of that in 2004. That is the lowest reported catch from Estonian coastal waters. In contrast, the landings from the German Baltic marine fishery in 2013 (41.8 t) remained at the level of 30% of that reported in 2001 (136.6 t; ICES, 2013). In Lithuania, the recorded landings for 2011 were very low due to low stocks and fishing effort (ICES, 2013).

The collapse in official catches at the beginning of the second half of the 1970s and observed throughout the 1980s can partly be explained by the economic difficulties of the last decade of the Soviet period. Our interviews revealed that probably ~40% of the catch was unreported during this period. As eel had a high value, it is obvious that fishers did not pass all their catches to the state purchase and this resulted in reduced official catches. Still, different fishing areas had different economic and regulative framework, which resulted in different motivation to report the catch. Fishers in areas such as the western islands worked in collective farms and had concrete fishing plans (demands) for eel. These ranged from tens of kilograms up to a few tonnes, depending on year. Of course, completing plans called for more accurate records and thorough control. However, if the plan was filled before the end of the fishing season, the remaining catch went very often unrecorded. The last happened also in the areas that did not operate under collective farms (e.g. Pärnu in southwest Estonia), as there was no

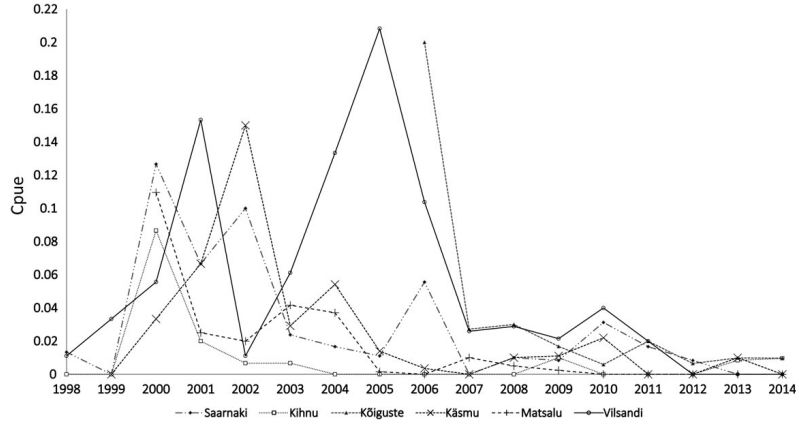

Figure 5. Estonian Marine Institute monitoring data (cpue, N/fyke day) for small fykenets.

Table 1. The total catch (kg) of small fykenets (SFN).

Year	2008	2009	2010	2011	2012	2013	2014
SFN total catch	654.5	707.5	427.6	296.4	166.8	124.6	87.6

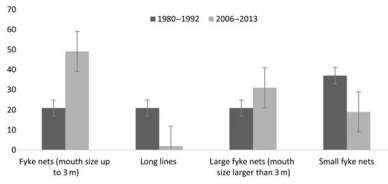

Figure 6. Comparison of fishing gear used (percentage) in professional coastal eel fishery in periods 1980–1992 and 2006–2013.

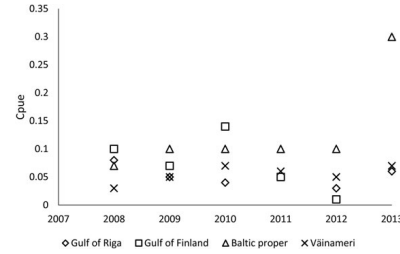

Figure 7. Cpue (kg per harvest) of professional small fykenets from all research areas (2008–2013).

motivation to report and deliver to state this highly valued fish. So, in areas operated under area fishery management institutions, it was common not to record any of the eels caught. In conclusion, eel fishing was widespread in all coastal areas of Estonia in the 1980s, but eel fishers used this most valued species often as an item of exchange for other goods or services. The change in political regime at the beginning of the 1990s and a concurrent disarrangement in report management ensured that some of the reports from that interval are missing or underestimated. The sudden rise in the catch records in the second half of the 1990s can be explained with the increase of fishing pressure, improvement of fishing gear (Vetemaa *et al.*, 2006), and improvement in registering the catches. Based on our interviews with fishers, it can be concluded that, in Estonia, there are no professional fishers any more for whom eel is the most important target species. In other words, nowadays, income from eel is incidental and relatively unimportant.

Interviewed fishers also proposed that the increase in cormorant numbers played a role in the decline of the eel stocks in the coastal waters. However, evidence was not that easy to find. Still, according to Rattiste (2014), the number of cormorant nests in Estonia has risen from 1 (1983) to 16 136 (2014). Eschbaum *et al.* (2003) state that, in 1998, 3.21 t ($s = 0.048$) of eel was consumed by cormorants in the Väinameri area. This is large amount—taking into account that the official landings in this area for the same year were 4.5 t. Vetemaa *et al.* (2010) found that cormorant colonies ($n = \sim 5600$ individuals in 2005) based on Käina Bay (9 km^2 area in the south-eastern coast of Hiiumaa, Väinameri area) were responsible of 1.7 t daily fish intake in the spring–summer period. However, the most important feeding areas for the cormorant are in the open waters (Carpentier *et al.*, 2009; Vetemaa *et al.*, 2010) during daytime and since cormorants favour most abundant species in their diet (Vetemaa *et al.*, 2010), the feeding pressure on eel might

be overestimated. In conclusion, most likely cormorants play a role in the decline of eel stocks in Estonian coastal waters, but, due to the lack of data, it is impossible to predict the size of the impact.

The decline of eel stocks is also clearly visible by the greatly reduced effort in recreational fishery. Since 2005, the total catch has fallen from 479 to 15 kg in 2012. However, according to the catch and effort data from 2008 to 2011, the cpue of recreational longlines had increased compared with earlier years (Bernotas, 2012). This could be explained by the decreased number of recreational fishers, and the hypotheses that probably only most experienced men still keep fishing. And since only their catch data remain, cpue figures have grown. In 2009, catch was reported through the recreational fishing database in 31 times, whereas in 2013 the same number was only 3, all coming from the Gulf of Riga. The overall lack of reports has been a trend over the last few years, and the only explanation for this situation is the absence of penalties applied to the recreational fishers not reporting their landings.

Historically, the most productive areas for eel fishing in the coastal waters of Estonia have been Väinameri and the Gulf of Riga. It is presumed that most of the eels caught in these areas derive from the natural stock, but there might be many silver eels with a stocked origin too, descending from the Narva RBD on their spawning run to the Sargasso Sea. This hypothesis is based on the fact that 3 of 1498 stocked eels tagged in the Narva RBD between 2007 and 2013 have been recaptured from the Baltic Sea, including one from the Danish coast (Järvalt *et al.*, unpublished data). The number of eels with a stocked origin tagged annually since 2007 ($n = \sim 214$) in Narva RBD is insufficient as the return rate of the tags from the coastal areas was very low (0.2%) for making more confident conclusions. It was found that in the coastal waters of Sweden, the landings of eel declined, while the cpue showed relative stability in the period 1970–2000. One of the reasons discussed was the possible migration of stocked eels from Baltic countries, later caught by Swedish fishers (Andersson *et al.*, 2012).

The number of small fykenet licences specially meant for professional eel fishing has been reduced by 50% over the last 7 years, while the cpue values have stayed quite steady (Figure 7).

It is known that fishers having the historical fishing rights for small fykenets purchase the licences, but never or very seldom use the gears for fishing. That is because the fishing fee is relatively cheap (in 2013, it was 0.95€ per one fykenet in a year) and the estimated catch is low (ICES, 2013). However, if fishers do not redeem the licences every year, their historical fishing rights get lost. As brought out in the results, 70% of the coastal fishers questioned in the survey revealed that they have not used small fykenets in the last 5 years. The most common reason was that the catch is very low or non-existent compared with the amount of work involved with setting up the gears. Compared with the 1980s, the use of small fykenets and longlines in professional eel fishing has decreased significantly (Figure 6).

Estonia is almost at the northeastern boundary of eel's geographical distribution, and the natural stocks compared with West-European countries are marginal. Today, eel is regarded mostly as side-catch, and is therefore unimportant in the Estonian marine fishery. Considering the overall strong stock decline, it can be prognosticated that the economic importance of the species will not grow in future. A restocking programme for the coastal areas has been under consideration in the Environmental Ministry, but it is too early to predict whether, or if at all, it will be implemented.

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References

Andersson, J., Florin, A., and Petersson, E. 2012. Escapement of eel (*Anguilla anguilla*) in coastal areas in Sweden over a 50-year period. ICES Journal of Marine Science, 69: 991–999.

Aps, R. 1996. Estonian Fisheries 1996. AS Expo Balticum Ltd. Tallinn. 131 pp.

Bernotas, P. 2012. An indirect method to estimate the abundance of European eel in shallow lakes based on mark-recapture data and CPUE of long lines. Dissertation. Estonian University of Life Sciences, Centre for Limnology. 39 pp.

Carpentier, A., Marion, L., Paillisson, J. M., Acou, A., and Feunteun, E. 2009. Effects of commercial fishing and predation by cormorants on the *Anguilla anguilla* stock of a shallow eutrophic lake. Journal of Fish Biology, 74: 2132–2138.

Dekker, W. 2003. Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? Fisheries Management, 1979: 365–376.

Eschbaum, R., Veber, T., Vetemaa, M., and Saat, T. 2003. Do Cormorants and Fishermen Compete for Fish Resources in the Väinameri (Eastern Baltic) Area? *In* Interactions Between Fish and Birds: Implications for Management. Ed. by I. G. Cowx. Blackwell Publishing Ltd. 384 pp.

HELCOM. 1996. Third Periodic Assessment of the State of the Marine Environment of the Baltic Sea, 1989–93; Background Document. Baltic Sea Environment Proc, No. 64B. 252 pp.

ICES. 1977. ICES Statistical Rectangle Coding System. ICES Document CM 1977/Gen: 3. 6 pp.

ICES. 2009. Report of the Study Group on Anguillid Eels in Saline Waters (SGAESAW), 16–18 March 2009, Sackville, Canada; 3–5 September 2009, Gothenburg, Sweden. ICES CM/DFC: 06. 183 pp.

ICES. 2010. The Report of the 2010 Session of the Joint EIFAC/ICES Working Group on Eels, September 2010. ICES CM 2009/ACOM:18. Country Reports. 198 pp.

ICES. 2013. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL), 18–22 March 2013 in Sukarietta, Spain, 4–10 September 2013 in Copenhagen, Denmark. ICES CM 2013/ACOM:18. 851 pp.

ICES. 2014. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eel, 3–7 November 2014, Rome, Italy. ICES CM 2014/ACOM:18. 203 pp.

Järvalt, A. 2008. Eel management plan. Report. 26 pp. Ministry of Environment. http://www.envir.ee/sites/default/files/elfinder/article_files/kavajaheakskiitmiseotsus03.12.2009.pdf.

Kint, P. 1940. Kalandus 1939. Eesti Kalandus. Estonian Fishery, 4/5: 85–102.

Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K., and Ojaveer, H. 2008. Gulf of Riga and Pärnu Bay. *In* Ecology of Baltic Coastal Waters. Ecological Studies 197, pp. 217–239. Ed. by U. Schiewer. Springer, Berlin. 419 pp.

Orav-kotta, H., Kotta, J., and Kotta, I. 2004. Comparison of macrozoobenthic communities between the 1960s and the 1990s—2000s in the Väinameri, NE Baltic Sea. Proceedings of the Estonian Academy of Sciences. Biology Ecology, 53: 283–291.

Pihu, E., and Turovski, A. 2001. Eesti mageveekalad. Freshwater fishes of Estonia. Kalastaja Raamat. 240 pp.

Pitkänen, H., Lehtoranta, J., and Peltonen, H. 2008. The Gulf of Finland. *In* Ecology of Baltic Coastal Waters. Ecological Studies 197, pp. 285–304. Ed. by U. Schiewer. Springer, Berlin. 419 pp.

Rattiste, K. 2014. Kormorani levik ja arvukus Eestis 2014. The distribution and abundance of the cormorant in Estonia 2014. Töövõtulepingu nr. 3-8/91 aruanne. Tartu 2014. Report. 31 pp. http://seire.keskkonnainfo.ee/attachments/article/3317/Kormorani%20levik%20ja%20arvukus%20Eestis%202014.pdf.

Simon, J., Ubl, C., and Dorow, M. 2013. Growth of European eel *Anguilla anguilla* along the southern Baltic coast of Germany and implication for the eel management. Environmental Biology of Fishes, 96: 1073–1086.

Suursaar, Ü., Kullas, T., and Otsmann, M. 2001. The influence of currents and waves on ecological conditions. Proceedings of the Estonian Academy of Sciences Biology Ecology, 50: 231–247.

Vetemaa, M., and Eero, M. 2005. Fishery in the Gulf of Riga: the structure and catch statistics. *In* Fishes and fisheries of the Gulf of Riga, pp. 26–38. Ed. by T. Saat and H. Ojaveer. University of Tartu, Tartu.

Vetemaa, M., Eero, M., Järv, L., and Saat, T. 2002. Estonian coastal fishery 1996–2000. *In* Fishes and Fisheries of the Väinameri, pp. 103–121. Ed. by T. Saat. University of Tartu, Tartu.

Vetemaa, M., Eschbaum, R., Albert, A., Saks, L., Verliin, A., Jürgens, K., and Saat, T. 2010. Changes in fish stocks in an Estonian estuary: Overfishing by cormorants? ICES Journal of Marine Science, 67: 1972–1979.

Vetemaa, M., Eschbaum, R., and Saat, T. 2006. The transition from the Soviet system to a market economy as a cause of instability in the Estonian coastal fisheries sector. Marine Policy, 30: 635–640.

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II

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ORIGINAL ARTICLE

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Age and growth of European eel, *Anguilla Anguilla* (Linnaeus, 1758), in Estonian lakes

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Summary

To investigate the difference in growth rates of eels in the studied water bodies (Võrtsjärv, Ülemiste, Saadjärv, Vagula, Kaiavere and Kuremaa lakes, all in Estonia), 828 individual eel otoliths from the years 1999–2004 and 2008–2012 were examined for age determination. *Anguilla anguilla* captured in Lake Võrtsjärv mostly by professional fyke nets (mesh size >36 mm in the cod end) showed the best growth rate (gR = 6.9 cm/year) and had a high Fulton condition factor (*K* = 0.19), indicating suitable growth conditions in the lake. However samples caught using the same type of gear from the smaller lakes situated near Võrtsjärv, showed much slower gR (3 cm/year) and lower *K* (0.17) growth rates. The slowest gR (2.6 cm/year) was observed for specimens caught in Lake Kuremaa. Stocking densities are much higher in the small lakes of the region and have a direct effect on the growth rates.

1 | INTRODUCTION

Aging of fish is principally determined by counting and verifying the growth zones (annual marks, *annuli*) in the hard parts of the fishes (Bagenal & Tesch, 1978). Different structures can be used, such as the scales, bones or otoliths. To determine the age of European eel, *Anguilla anguilla*, researchers use sagittal otoliths (Vøllestad, Lecomte-Finiger, & Steinmetz, 1988). Age determination for *anguillids* is usually based on observing the number of annual rings present on the otolith (Beentjes & Jellyman, 2015). Otoliths can characterize the entire life-cycle of the studied fish. Depending upon the environment (ICES, 2009) the formation of annuli may also differ, making it possible to draw parallels between different biotopes inhabited by the eel.

Age determination based on examination of otoliths is relatively new in Estonian fisheries science. Apart from Rohtla et al. (2014), Rohtla, Taal, Svirgsden, and Vetemaa (2015) with research on burbot (*Lota lota*) and ide (*Leuciscus idus*), respectively, there are no other recent scientific publications. A paper was published by Kangur (1998) regarding the growth rates of eels in Lake Võrtsjärv as a part of a larger study concerning this species. Unfortunately, the methodology used to measure the growth rates was not mentioned.

Eel landings have decreased rapidly throughout Europe since the 1960s (ICES, 2014). The same applies for the coastal waters of Estonia, where eel landings have declined by over 90% compared to the beginning of the 2000s (Bernotas et al., 2015). However, eel landings in freshwaters have remained steady for the past 5 years (averaging 15 tonnes/year; ICES, 2015), as these populations rely completely on stocking (ICES, 2014). Apart from Lake Ülemiste, all studied waterbodies (Figure 1) have annual stocking programmes (Table 1). According to the Estonian Eel Management Plan (EMP; Järvalt, 2008), Estonia is divided into two eel management units – West-Estonian River Basin District (RBD) and Narva RBD (Järvalt, 2008). Eels have been stocked in Lake Võrtsjärv since the 1950s and in other Narva RBD waterbodies since the beginning of 2000s (ICES, 2014). Both glass eels and elvers have been stocked in these lakes. As the purpose of stocking eels in the Narva RBD water bodies is to secure the reproduction of the species (Järvalt, 2008), an understanding of age and growth of the eels in freshwater habitats is necessary. In this paper we present an analysis of the different growth parameters of *A. anguilla* in Estonian lakes and discuss the environmental and anthropogenic factors influencing these parameters.

2 | MATERIAL AND METHODS

2.1 | Study area

Our study area consisted of six lakes, of which five are situated in Narva RBD and one in the West-Estonian RBD (Figure 1; Table 2).

The eels inhabiting Lake Ülemiste were stocked in 1986 as glass eels and therefore of known ages – 17 and 18 years. These glass eels originating from France were originally destined for stocking in Lake Võrtsjärv, but due to logistical complications were released into the closest water body to the airport, in this case the Ülemiste. The exact amount of eels stocked in the Ülemiste is not known.

FIGURE 1 Location of studied lakes in Estonia. 1 – Võrtsjärv; 2 – Ülemiste; 3 – Saadjärv; 4 – Vagula; 5 – Kaiavere; 6 – Kuremaa

TABLE 1 Average annual number of stocked eels (*Anguilla anguilla*) per hectar (period 1999–2012) in five studied Estonian lakes (excluding Ülemiste; ICES, 2015)

Lake	Period	sp/ha/year
Vortsjarv	1999–2012	12
Saadjarv	2000–2012	33
Kaiavere	2010–2012	58
Kuremaa	2002–2012	26
Vagula	2001–2012	21

2.2 | Data

The 828 otoliths used in this study originate from the eel otolith collection of the Centre for Limnology of Estonian University of Life Sciences dating back to 1999 (Table 3). Based on the life stage at stocking (glass eel or elver), the otoliths collected from the Võrtsjärv eels were divided into two groups. The glass eel group (Võrtsjärv G) contains otoliths collected during the period 1999–2003. The elver group (Võrtsjärv E) includes otoliths from 2010 to 2012. All individuals were caught with professional fyke nets (mesh size >36 mm in the cod end). The eels were measured for total length (TL, cm) and total weight (TW, g), and the date of capture recorded. Fulton's condition factor *K* (Fulton, 1904) was calculated for each analysed specimen. The annual gain in length was calculated according to the formula:

$$gR = \frac{(L - x)}{t}$$

where gR is the mean annual length increment in cm per year. *L* is the total length of the eel, *X* is the total length of the eel at stocking and *t* is the established otolith age (Svedäng, Neuman, & Wickström, 1996). *X* = 7 cm for glass eels and *X* = 15 cm for elvers.

Analysis of variance (ANOVA) and the Tukey HSD test were used to assess differences between observed variables (mean length and age of eels, Fulton condition factor and annual growth, coefficient of variation differences) in the different lakes; Pearson correlation coefficient was used to test the relationship between annual growth

TABLE 2 Characteristics of studied eutrophic water bodies in Estonia (Järvet, 2004; Mäemets, 1977; Tamre, 2006)

Name	Catchment area (km^2)	Surface area (km^2)	Mean depth (m)	Max depth (m)	Stratified
Vortsjarv	3,104	270	2.8	6	No
Ulemiste	99.2	9.6	2.5	6	No
Saadjarv	31.9	7.2	8	25	Yes
Vagula	495	5.1	5.3	11.5	Yes
Kaiavere	92.2	2.5	2.5	4.5	No
Kuremaa	25.4	4.0	5.9	13.8	Yes

TABLE 3 Number of *Anguilla anguilla* otoliths used for age determination in six studied Estonian lakes, including years when sampled

	1999	2000	2001	2002	2003	2004	2008	2009	2010	2011	2012	Total (N)
Vortsjarv	43	90	72	4	6				3	148	42	408
Ulemiste					11	12						23
Saadjarv		14			1		6	19	10	22	45	117
Vagula			7						46	19	17	89
Kaiavere									61	18	6	85
Kuremaa				10			27	17	12	15	25	106
	43	104	79	14	18	12	33	36	132	222	135	828

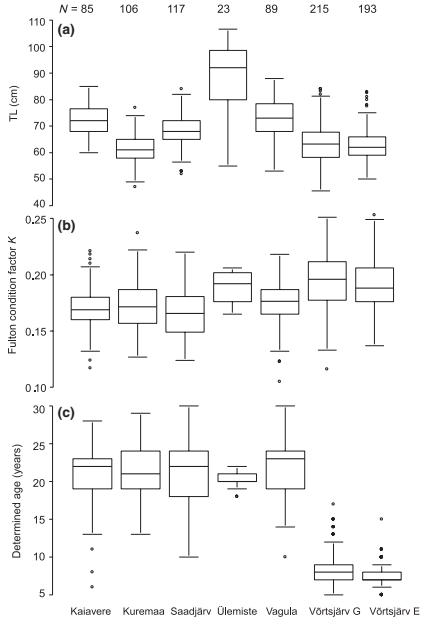

FIGURE 2 Mean parameters of *Anguilla anguilla* captured in different periods (Kaiavere 2010–2012; Kuremaa 2002–2012; Saadjärv 2000–2012; Ülemiste 2003–2004; Vagula 2001–2012; Võrtsjärv G 1999–2003; Võrtsjärv E 2010–2012) in selected Estonian lakes: (a) Length distributions; (b) calculated Fulton condition factors (*K*) for the analysed specimens; (c) age determination in analysed specimens. Box = 25% and 75% quartiles and TL (a), *K* (b), *t* (c) median; bars = maximum and minimum values in analysed samples

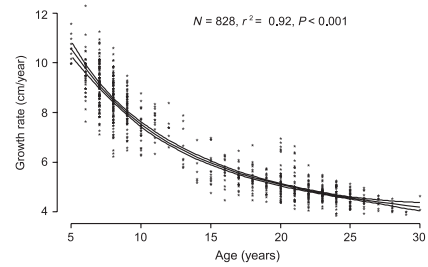

FIGURE 3 Relationship between annual growth and validated age of *Anguilla anguilla* (*N* = 828) in Estonian lakes, all captures between 1999–2012

and age. A *t* test was used for testing differences between different Coefficient of variation (CV) groups.

Statistical analyses were conducted using 2.14.1 (R Core Team, 2014) and Statsoft STATISTICA 12. (http://www.statsoft.com/Products/STATISTICA/Product-Index).

2.3 | Extraction and preparation of otoliths. Age determination

Sagittae otoliths were extracted, cleaned and stored in microtubes filled with glycerine. Slight improvements were made to the 'burning and cracking' method (Hu & Todd, 1981), whereby the otolith was fractured through the core. If the core was not revealed, additional polishing of the otolith was needed. Burning was done in the flame of a spirit lamp on the blade of a scalpel. After cooling, the otolith was fixed to a base filled with modelling paste.

The Motic SMZ-143-FBGG stereomicroscope with a Moticam 2000 and Moticam 5 camera was used for viewing and photographing the otoliths. Motic Images Plus 2.0ML (http://www.motic.com/As_microscope_software_r/product_230.html) software was used for image post-processing.

Three to four different persons participated in the age reading process. A mean value was calculated using all age readings associated with the otolith. To measure the aging precision, the methodology described by Campana (2001) was used. Coefficient of variation (CV) was calculated using the formula:

$$CV_b = 100\% \times \frac{\sqrt{\sum_{a=1}^{R} \frac{(X_{ab}-X_b)^2}{R-1}}}{X_b}$$

where CV_b is the age precision estimate for the *b*th fish. X_{ab} is the *a*th age determination of the *b*th fish and X_b is the mean age estimate of the *b*th fish, and *R* is the number of times the age of each fish was determined. Campana (2001) also recommended using CV of 5% as an indicator of good aging precision.

3 | RESULTS

The length distribution of eels (*N* = 828) was compared among the studied lakes (ANOVA $F_{5,828} = 100.6$, $p < .001$). Specimens caught in Lake Ülemiste had a significantly higher mean TL (TL = 87.8 cm; *N* = 23) than eels in the other lakes (Tukey HSD, *Q* = 18; $p < .01$; Figure 2a). The shortest eels were found in the samples from lakes Kuremaa (TL = 61.6 cm; *N* = 106) and Võrtsjärv (TL = 63.1 cm; *N* = 408).

Comparing the calculated Fulton condition factors among the studied specimens revealed highest mean values for eels caught in lakes Võrtsjärv and Ülemiste (*K* = 0.19, *N* = 401; Figure 2b).

The mean determined age (*t*) of an eel (Figure 2c) did not differ significantly for specimens caught in lakes Saadjärv, Kuremaa, Kaiavere and Vagula (*t* = 21.2 years, *N* = 399, ANOVA $F_{3,395} = 0.9$, $p = .5$). In Võrtsjärv G the mean age of captured individuals was *t* = 8.44 (*N* = 215)

TABLE 4 Number of age readers and samples of *Anguilla anguilla* analysed in six studied Estonian lakes

Water body	N_{reader}	$N_{samples}$	CV mean (%)
Ulemiste	3	23	3
Vortsjarv	4	408	4
Kuremaa	3	106	4
Saadjarv	3	117	7
Kaiavere	2	85	7
Vagula	3	89	8.5

Mean coffecient of variation (CV) of the average percent error describes the precision of age determination among the age readers.

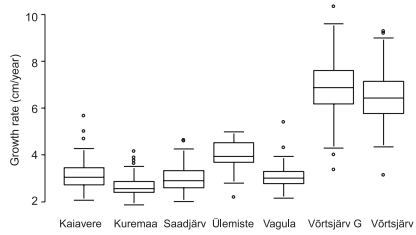

FIGURE 4 Differences in *Anguilla anguilla* growth rates in six studied Estonian lakes. Box = 25% and 75% quartiles and median growth rate; bars = maximum and minimum observed growth rates in analysed samples (N = 828)

years, but was 0.94 years younger (t = 7.5, N = 193) in the Võrtsjärv E group, with the difference statistically significant (p = .03). In Lake Ülemiste the known stocking-based age of the eels (17–18 years) was overestimated by 2–3 years (average t = 20.2).

The relationship between annual growth and age in our entire database (N = 828) showed a strong negative correlation (r^2 = −.92, p < .001, Figure 3). When annual growth in the studied lakes was compared, we did not find any statistical differences in Kaiavere, Saadjärv and Vagula (ANOVA $F_{2,289}$ = 1.6, p = .2). However, the gR values for the Võrtsjärv G and Võrtsjärv E groups (6.9 cm/year and 6.5 cm/year, respectively) differed significantly (ANOVA $F_{1,6}$ = 78.4, p < .001) from gR values in the other studied lakes (Table 4). When compared to the other studied lakes, Lake Võrtsjärv glass eels grew 3.88 cm/year faster (Figure 4).

Age reading precision was the most accurate (CV 3–4%) in Võrtsjärv, Kuremaa and Ülemiste and somewhat lower (CV 7–8.5%) in the other studied lakes (Table 4). There were significant differences in the age determination among the age readers for Kaiavere (N_{reader} = 2; t = 2.6; df = 150; p = .009), Kuremaa (N_{reader} = 3; ANOVA $F_{2,306}$ = 4.2, p = .01), and Võrtsjärv (N_{reader} = 3; ANOVA $F_{3,164}$ = 3.3, p = .02; N_{reader} = 4; ANOVA $F_{2,252}$ = 14.3, p < .0001). Age determination did not vary significantly among age estimators for Ülemiste (N_{reader} = 3; ANOVA $F_{2,66}$ = 2.2, p = .1), Saadjärv (N_{reader} = 3; ANOVA $F_{2,294}$ = 1.4, p = .2), and Vagula (N_{reader} = 3; ANOVA $F_{2,252}$ = 0.6, p = .5).

4 | DISCUSSION

In Lake Võrtsjärv our estimations of the growth rate for *A. anguilla* that were stocked as glass eels (group Võrtsjärv G, period 1999–2003, mean gR = 6.9 cm/year) were higher than those observed by Kangur (1998) (5.9 cm/year). According to Sinha and Jones (1967) and Tesch (2003), population density can have a considerable effect on the eel growth rate: in more crowded populations the growth rate tends to be lower. In Võrtsjärv, the population density decreased from 35 sp/ha in 1965–2001 to 12 sp/ha in 2002–2010 (ICES, 2010). The legal size limit for commercial fishery of eel was lowered in 2002 from TL = 60 cm to TL = 55 cm. Allowing stronger fishing pressure and younger individuals to be caught by the fishermen could have caused the rise in the growth rate after this change. When compared to eels caught in small German lakes (Simon, 2007), our estimated growth rates (excluding Võrtsjärv) were exceptionally lower. Age of the studied individuals could play a crucial role here, since the growth rate decreases with age (Figure 3). The difference was most probably caused by the age difference of the studied specimens in the different lakes, as growth of the older individuals is assumed to be slower (Simon, 2007). The maximum age class of eels examined by Simon (2007) was 14 years. The mean estimated age for the individuals studied in the small lakes of Narva RBD exceeded 20 years, while the mean determined age for individuals caught in Lake Võrtsjärv was 8 years. Thus, it is not surprising that the estimated mean growth rate of *A. anguilla* was highest in Lake Võrtsjärv and lowest in the small lakes of Narva RBD.

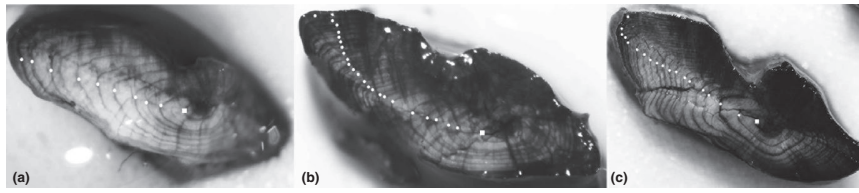

FIGURE 5 *Anguilla anguilla* otoliths collected from lakes (a) Võrtsjärv (t = 9 years); (b) Kaiavere (t = 23 years); (c) Ülemiste (t = 17 years). Square = zero band (first growth check outside the nucleus; ICES, 2009). Note faint stress rings formed on each otolith

The estimated growth rate of eels in Lake Võrtsjärv was also higher than the mean values documented in Norway (6.2 cm/year; Vøllestad & Jonsson, 1986), Poland (4.1 cm/year; Nagiec & Bahnsawy, 1990), Denmark (3.6 cm/year; Bisgaard & Pedersen, 1991), France (5.3 cm/year; Panfili, Ximenes, & Crivelli, 1994) Ireland (1.5–6.2 cm/year; Arai, Kotake, & McCarthy, 2006), and Germany (4.5 cm/year; Simon, 2007).

Previous studies by Simon and Dörner (2013), and Simon, Dörner, Scott, Schreckenbach, and Knösche (2013) showed that *A. anguilla* stocked into lakes as elvers (TW = 6.6 g at stocking) had some difficulties adapting to natural prey in the first years, reflected by lower growth rates when compared to the group stocked as glass eels. However, after the third or fourth year post-stocking, the growth rates between the two different groups equalized. Our results showed that the condition factors of the specimen in the Võrtsjärv G and E groups were very close (0.19 ± 0.002).

From May to September, the water temperature usually stays above 10°C in Lake Võrtsjärv (Järvet, 2004). Eels feed actively during this period (Sinha & Jones, 1967). Due to the shallowness and large surface area, the waters in lakes Võrtsjärv and Ülemiste are well mixed and aerated in the ice-free period. Nevertheless, wind-free and hot periods in the summer can cause hypoxia in the bottom layer of both lakes (Järvet, 2004; Ott, 2012). Hypoxic conditions can relate to increasing levels of stress in fish. Tzeng, Wu, and Wickström (1994) found that false annuli formation on eel otoliths is related to short-term stress. This could also explain the false annuli observed on eel otoliths in the Võrtsjärv and Kaiavere lakes as well as in Lake Ülemiste (Figure 5). In the Ülemiste, cyanobacterial blooms have been common in past summer decades (Pedusaar, 2010). Harmful effects of cyanobacterial blooms on fishes are widely acknowledged (Havens, 2008). Eels have a pH optimum of 7–8 (Tesch, 2003), but during cyanobacterial blooms the water pH can rise above 10 (Gao, Cornwell, Stoecker, & Owens, 2012) and remain at that level for weeks, which could add to the stress caused by the low oxygen content and form false annuli on an otolith.

In Lake Kaiavere, in addition to a fluctuating oxygen content and high water pH (mean value = 8.6 in 2011; Ott, 2011) in the summer months, an unidentified bacterial infection has been observed on eels. This disease has also been found on specimens collected from lakes Kuremaa, Saadjärv and Vagula. It can be assumed that the infection occurs when the immune system of the eel is weakened. Changes in water temperature, population density and stress all influence the immune system parameters (Magnadottir, 2006; Uribe, Folch, Enriquez, & Moran, 2011). The rise in the level of stress potentially contributes to the formation of false annuli on otoliths, thus causing an overestimation of the eel age.

The age determination variation (CV) values were above the recommended 5% for most of the studied small lakes. The combination of false annuli and high age of the fish could lead to some aging errors. However, analysing the age reading data showed that the age determination CV values of samples from Ülemiste, Saadjärv and Vagula did not differ significantly among the age readers. No variation between the age readers in samples considering Lake Ülemiste was expected since the sample size was low (N = 23) and the known eel age was 17–18 years. In the studied small lakes a different method of age verification is needed to confirm the relatively high ages (t = 21 years) determined. As such, mass marking was already carried out in both Võrtsjärv and the small lakes of Narva RBD in 2014–2015 (Silm, Järvalt, Mäe, & Bernotas, 2015) and 2016 (M. Silm, unpublished data), and the growth rates of the eel can be corrected as soon as the first marked eels begin to appear in official catches, anticipated to be in the year 2019.

The difference in the condition factor (K) values shows that between the studied lakes, eel growth conditions are most suitable in lakes Võrtsjärv and Ülemiste. These lakes share similar characteristics when it comes to feeding objects and water quality (Järvet, 2004; Ott, 2012; Pedusaar, 2010). However, the length variation was greater among the specimens from Ülemiste (Figure 2a). As the age of eels in Ülemiste is known from the stocking history (17–18 years) with little variation, this shows that the growth rate can vary significantly among specimens stocked in the same year.

5 | CONCLUSION

Võrtsjärv has very good growth conditions for eels, considering the observed mean K-value (0.19) and mean growth rate of glass eels (6.9 cm/year) and elvers (6.5 cm/year). Our study showed that the eels in the small lakes of Narva RBD grew much more slowly (mean growth rate 2.9 cm/year), but in these lakes age overestimation due to false annuli on the otoliths might have occurred. A possible solution for the problem would be mass marking of all individuals before stocking into these lakes. Such mass marking was already carried out in both Võrtsjärv and the small lakes of Narva RBD in 2014–2016, and the eel growth rates can be corrected as soon as the first marked eels begin to appear in official catches, anticipated in the year 2019.

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REFERENCES

Arai, T., Kotake, A., & McCarthy, T. K. (2006). Habitat use by European eel *Anguilla anguilla* in Irish waters. *Estuarine, Coastal and Shelf Science*, *67*, 569–578.

Bagenal, T. B., & Tesch, F. W. (1978). Age and growth. In T. B. Bagenal (Ed.), *Methods for assessment of fish production in freshwaters*, 3rd edn (pp. 101–136). Oxford, UK: Blackwell Scientific Publications.

Beentjes, M. P., & Jellyman, D. J. (2015). Growth patterns and age validation from otolith ring deposition in New Zealand longfin eels Anguilla dieffenbachii recaptured after 10 years at large. *Journal of Fish Biology*, *86*, 924–939. doi:10.1111/jfb.12601

Bernotas, P., Vetemaa, M., Saks, L., Eschbaum, R., Verliin, A., & Järvalt, A. (2015). Dynamics of European eel landings and stocks in the coastal

waters of Estonia. *ICES Journal of Marine Science*, *73*(1), 84–90. Retrieved from http://doi.org/10.1093/icesjms/fsv245

Bisgaard, J., & Pedersen, M. I. (1991). Mortality and growth of wild and introduced cultured eels (*Anguilla anguilla* (L.)) in a Danish stream, with special reference to a new tagging technique. *Dana*, *9*, 57–69.

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, *59*, 197–242. doi:10.1111/j.1095-8649.2001.tb00127.x

Fulton, T. W. (1904). *The rate of growth of fishes*. Twenty-second Annual Report, Part III. Edinburgh: Fisheries Board of Scotland. pp. 141–241.

Gao, Y., Cornwell, J. C., Stoecker, D. K., & Owens, M. S. (2012). 2012: Effects of cyanobacterial-driven pH increases on sediment nutrient fluxes and coupled nitrification-denitrification in a shallow fresh water estuary. *Biogeosciences*, *9*, 2697–2710. doi:10.5194/bg-9-2697-2012

Havens, K. E. (2008). Cyanobacteria blooms: Effects on aquatic ecosystems. In Cyanobacterial Harmful Algal Blooms: State of the Science and Research Needs. *Advances in Experimental Medicine and Biology*, *619*, 733–747 doi: 10.1007/978-0-387-75865-7_33

Hu, L. C., & Todd, P. R. (1981). An improved technique for preparing eel otoliths for ageing. *New Zealand Journal of Marine and Freshwater Research*, *5*, 445–446.

ICES (2009) *Workshop on Age Reading of European and American Eel (WKAREA)*. 20-24 April 2009, Bordeaux, France. ICES CM 2009 \ ACOM: 48, pp. 66.

ICES (2010). *Report of the Workshop on Baltic Eel (WKBALTEEL)*. 2–4 November 2010, Stockholm, Sweden. ICES CM 2010/ACOM:59, pp. 97.

ICES (2014). *Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels*. 3–7 November 2014, Rome, Italy. ICES CM 2014/ACOM:18, pp. 203.

ICES (2015). *Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL)*. 24 November–2 December 2015, Antalya, Turkey. ICES CM 2015/ACOM:18, pp. 130.

Järvalt, A. (2008). Eel management plan. Ministry of Environment. Report, pp 26. Retrieved from http://www.envir.ee/sites/default/files/elfinder/article_files/kavajaheakskiitmiseotsus03.12.2009.pdf

Järvet, A. (2004). Hydrology of Lake Võrtsjärv. In J. Haberman, E. Pihu, & A. Raukas (Eds.), *Lake Võrtsjärv (105–139)* (pp. 105–139). Tallinn: Estonian Encyclopaedia Publishers.

Kangur, A. (1998). European eel, *Anguilla anguilla*, (L.) fishery in Lake Võrtsjärv: Current status and stock enhancement measures. *Limnologica*, *28*(1), 95–101.

Mäemets, A. (1977). *Eesti NSV järved ja nende kaitse (The lakes of Soviet Estonia and their protection)*. Tallinn: Valgus. pp. 264.

Magnadottir, B. (2006). Innate immunity of fish (overview). *Fish & Shellfish Immunology*, *20*, 137–151.

Nagiec, M., & Bahnsawy, M. H. (1990). Age and growth of female eels, *Anguilla anguilla* L., in a Polish lake, Jeziorak Lake, Mazurian Lake District, Poland. *Aquaculture Research*, *21*, 459–470.

Ott, I. (2011). *Eesti väikejärvede seire (The monitoring of Estonian small lakes)*. Report. Tartu: Estonian University of Life Sciences. pp. 188. Retrieved from http://eelis.ic.envir.ee/seireveeb/aruanded/13174_aru11_aruande_tekst_sisukorraga.doc

Ott, I. (2012). *Eesti väikejärvede seire (The monitoring of Estonian small lakes)*. Report. Tartu: Estonian University of Life Sciences. pp. 169. Retrieved from http://eelis.ic.envir.ee/seireveeb/aruanded/14073_vaikejarvede_aruande_tekst_2012.doc

Panfili, J., Ximenes, M. C., & Crivelli, A. J. (1994). Sources of variation in growth of the European eel (*Anguilla anguilla*) estimated from otoliths. *Canadian Journal of Fisheries and Aquatic Science*, *51*, 506–515.

Pedusaar, T. (2010). *Ülemiste järve kui joogiveehoidla haldamine (Management of Lake Ülemiste as Drinking Water Reservoir)*. Dissertation. Tallinn: University of Technology. pp. 126. Retrieved from http://digi.lib.ttu.ee/i/file.php?DLID=483&t=1

R Core Team (2014). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Rohtla, M., Taal, I., Svirgsden, R., & Vetemaa, M. (2015). Oldtimers from the Baltic Sea: Revisiting the population structure and maximum recorded age of ide *Leuciscus idus*. *Fisheries Research*, *165*, 74–78 j.fishres.2015.01.001.

Rohtla, M., Vetemaa, M., Taal, I., Svirgsden, R., Urtson, K., Saks, L., … Saat, T. (2014). Life history of anadromous burbot (*Lota lota*, Linneaus) in the brackish Baltic Sea inferred from otolith microchemistry. *Ecology of Freshwater Fish*, *23*(2), 141–148. eff.12057.

Silm, M., Järvalt, A., Mäe, A., & Bernotas, P. (2015). *First results of mass marking of European eel (Anguilla anguilla) with alizarin red and SrCl2 in Estonia*. XV European Congress of Ichthyology, Porto, Portugal. 7 - 11 Sep, 2015. Frontiers Media, 100–101.

Simon, J. (2007). Age, growth, and condition of European eel (*Anguilla anguilla*) from six lakes in the River Havel system (Germany). *ICES Journal of Marine Science*, *64*(7), 1414–1422.

Simon, J., & Dörner, H. (2013). Survival and growth of European eels stocked as glass- and farm-sourced eels in five lakes in the first years after stocking. *Ecology of Freshwater Fish*, *23*, 40–48.

Simon, J., Dörner, H., Scott, R. D., Schreckenbach, K., & Knösche, R. (2013). Comparison of growth and condition of European eels stocked as glass and farm sourced eels in lakes in the first 4 years after stocking. *Journal of Applied Ichthyology*, *29*, 323–330.

Sinha, V. R. P., & Jones, J. W. (1967). On the age and growth of the freshwater eel (*Anguilla anguilla*). *Journal of Zoology*, *153*, 99–117.

Svedäng, H., Neuman, E., & Wickström, H. (1996). Maturation patterns in female European eel: Age and size at the silver eel stage. *Journal of Fish Biology*, *48*, 342–351.

Tamre, R. (2006). *Eesti järvede nimestik. Looduslikud ja tehisjärved*. Keskkonnaministeeriumi Info- ja Tehnokeskus (List of lakes in Estonia. Natural and artificial lakes. Ministry of Environment, Information Centre), Tallinn, Estonia. pp. 168. (in Estonian)

Tesch, F. W. (2003). 3.3.2 Age and growth, 5th edn. In J. E. Thorpe (Ed.), *The eel* (pp. 163–181). Oxford, England: Blackwell Science.

Tzeng, W. N., Wu, H. F., & Wickström, H. (1994). Scanning electron microscopic analysis of annulus microstructure in otolith of European eel, *Anguilla anguilla*. *Journal of Fish Biology*, *45*, 479–492.

Uribe, C., Folch, H., Enriquez, R., & Moran, G. (2011). Innate and adaptive immunity in teleost fish: A review. Review Article. *Veterinarni Medicina*, *56*(10), 486–503.

Vøllestad, L. A., & Jonsson, B. (1986). Life-history characteristics of the European eel *Anguilla anguilla* in the Imsa River. *Transactions of the American Fisheries Society*, *115*, 864–871.

Vøllestad, L. A., Lecomte-Finiger, R., & Steinmetz, B. (1988). Age determination of *Anguilla anguilla* (L.) and related species. *EIFAC Occas*, *21*, 1–28.

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III

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How do environmental factors affect the yield of European eel (*Anguilla anguilla*) in a restocked population?

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Fisheries

ABSTRACT

Restocking of European eel (*Anguilla anguilla*) is a widespread practice throughout Europe. Conditions during restocking activities and mortality related to restocking practices have been discussed, however, factors affecting these restocked populations afterwards are mostly not considered. In this study we used a machine learning method followed by generalized linear model to analyze long time eel restocking, commercial fishery and environmental data from Lake Võrtsjärv, Estonia, to detect whether significant relationships exist within these data. It was found that environmental parameters can have an effect on the commercial eel yield both retrospectively and during the particular fishing year. Considering that 7-year old eel was the most common age group in commercial catch, we introduced a 7-year gap between eel restocking and yield to study the most important abiotic and biotic factors during the first year of eel restocking that have an effect on the yield. According to our results, cyanobacterial biomass and summer water temperature during the year of restocking had the strongest negative impact on the yield 7 years after, while the number of restocked individuals and copepod biomass had a positive effect. During particular fishing year, however, the yield was most notably positively affected by total phosphorous concentration, number of individuals restocked 7 years before and metazooplankton biomass in the lake.

1. Introduction

Increasing anthropogenic pressures have multiple effects on freshwater ecosystems (Carpenter et al., 2011). Overexploitation of certain fish species, influence of different pollutants, habitat degradation, invasive species and physical modification of flow characteristics, each play a role in changing conditions both in freshwater lakes and rivers (Dudgeon et al., 2006). Most of these factors have a direct or indirect impact on the rise of such phenomena as eutrophication, dominance of cyanobacteria, increase in phosphorous concentrations, and high nitrogen fixation rates (Hecky et al., 2010; Mugidde et al., 2003). Besides, freshwater systems are also heavily affected by climate change (Mooij et al., 2005; Woodward et al., 2010). Global warming has been found to have a strong impact on eutrophication of fresh water lakes (Anneville et al., 2015) and has a positive influence on growth rates, dominance, distribution and activity of harmful cyanobacteria (Paerl and Huisman, 2009, 2008). The negative effect of hypoxia caused by eutrophication and cyanobacterial blooms on benthic fish species has been widely discussed in scientific literature (Diaz and Rosenberg, 1995; Paerl and Huisman, 2009; Pörtner and Peck, 2010).

A benthic species such as the European eel (*Anguilla anguilla*) is known to inhabit a wide variety of habitats from marine to fresh waters (Tesch et al. 2003). While eel is being a common species throughout Europe, its stocks have been declining rapidly during the last 40–50 years (Dekker, 2016). It is known that anthropogenic factors such as habitat loss, water pollution, commercial and recreational fisheries and migration obstacles (dams, weirs, pumping stations) play an important role in the decline (Dekker and Beaulaton, 2016). These factors affect eels most in the continental phase of the life cycle while environmental factors, such as climate change, mostly during the oceanic phase (Drouineau et al., 2018). However, as eels can spend most of their life in fresh water (Tesch et al., 2003) the environmental stressors affecting this period need to be studied thoroughly.

Eels may reach fresh waters via migration through river systems or by restocking. In Estonia, most of the fresh water eel population relies on annual restocking programme (Bernotas et al., 2016). While eels are known to be able to survive in unfavourable conditions (Tesch et al. 2003), their distribution in a water body still depends on habitat quality and accessibility as well as population characteristics (Laffaille, 2003). However, studies on environmental parameters affecting glass eels or

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elvers following restocking are hard to find.

For implementation of conservation measures, describing of changes in fish biomass and population dynamics or experimenting with "what if" scenarios, the fisheries science has been using different modelling approaches (Christensen and Walters, 2004; Methot and Wetzel, 2013; Pauly et al., 2000; Thorson, 2019). As complex freshwater ecosystems, such as large lakes, have numerous parameters influencing their fish communities, ecosystem modelling is the most suitable approach for predicting the potential effects of these interactions (Ficke et al., 2007). In Estonian freshwater fisheries context, modelling has been used to determine which abiotic and biotic factors control the changes in fish biomass in Lake Võrtsjärv (Öğlü et al., 2019).

The aim of this study was to investigate what are the most important environmental factors affecting the restocked eels directly after restocking and later in their growing phase. It was alsoassumed that the number of specimens restocked has the strongest influence on the yellow eel stock capacity. We asked what affects most the commercial yield, which indicates the stock size of eels 7 years after restocking when the age class becomes most prominent in the catches – the number of specimens restocked, the conditions at restocking or the conditions of the particular fishing year.

2. Material and methods

2.1. Study area

Võrtsjärv is a large, but shallow, eutrophic and turbid water lakeThe surface area of the lake is 27 000 ha, making it the second largest lake in the Baltic States (Järvet, 2004). Its drainage basin (3374 km^2) is situated in the Central Estonian depression of preglacial origin and is connected to the drainage basin of Lake Peipsi (47,800 km^2) through the outflowing Emajõgi River (Järvet, 2004). The small mean and maximum depths, 2.8 m and 6.0 m, respectively, make Võrtsjärv responsive for environmental changes. The water is alkaline and due to turbidity the visibility is low. The lake is covered with ice on average for 135 days, lasting from November until April (Tõnno et al., 2016). No significant trends in the ice cover duration were found (Nõges and Nõges, 2014). According to the Water Framework Directive typology, Võrtsjärv is a large calcareous shallow lake with most ecological status parameters falling into either "good" or "moderate" class (Tuvikene et al., 2011). During ice-free period, Secchi depth does not exceed 1 m. Phytoplankton is dominated by eutrophic and highly shade tolerant cyanobacteria from the genus *Limnothrix* (Janatian et al., 2019). According to the long-term annual phytoplankton primary production (208 ± 27 gC m^{-2} $year^{-1}$), Võrtsjärv is close to the nutrient-saturated production boundary for lakes determined by latitude where light limitation has the leading role (Nõges et al., 2011).

2.2. Fisheries

One lamprey species (*Lampetra planeri*) and 31 fish species permanently inhabit Võrtsjärv (Järvalt, 2003; Pihu, 1998). Eel, pikeperch (*Sander lucioperca*), pike (*Esox lucius*), and bream (*Abramis brama*) are the most important commercial species in the lake, while perch (*Perca fluviatilis*) and burbot (*Lota lota*) are of secondary commercial interest (Järvalt, 2003; Nõges et al., 2018).

The eel production of Võrtsjärv is entirely based on restocking of glass eels or elvers. The restocking programme started in 1956 and has continued to present day. Since 1980, restocking of eel has been annual (excluding years 1986, 1989, 1990 and 1993; Bernotas et al., 2020). The number of restocked individuals has been dependent on available financial resources and thus directly connected to the glass eel market prices (Bernotas and Silm, 2019). Eel is targeted by commercial fishery using fyke nets (mesh size in the cod end =18 mm) with the legal landing size being TL ≥ 55 cm. Commercial harvest is due to the legal size dominated by female yellow eels. The number of fyke nets used by the fishermen has stayed on a stable level (from 300 to 360) since 1971 (Nõges et al., 2018). The eel fishing season lasts from April to October. No data on the number of fishermen or companies is available for the Soviet time. The number of fishermen or companies operating the gear has changed during the last 10 years due to companies selling some of the licences however the number of gear has stayed the same (N = 322).

For calculation purposes, the amounts of restocked elvers were converted into *glass eel equivalents (GEE)* according to formula by Dekker (2015):

$$glass\ eel\ equivalents_{year-age} = elvers_{year,\,age} \times exp^{+M \times age}$$

where year = the year of observation, age = the mean age, and M = natural mortality between the glass eel and the elver stage. For M, an average value of 0.10 per year was used (Dekker, 2015).

2.3. Data collection

The data used in the models derives from 3 different sources. The commercial fisheries data (tonnes) is collected annually by the Ministry of Rural Affairs, the eel restocking data (numbers, kilograms) annually by the Ministry of Environment and the data on environmental variables by Estonian University of Life Sciences. The commercial fisheries and eel restocking data used in this study dates back to 1964 and 1956, respectively (Table 2). The data on water chemistry, phyto- and zooplankton biomass is available since 1964 and is collected at least once per month (Nõges et al., 2018). Benthic macroinvertebrate (BMI) samples are taken during ice-free period and sampled alive, processed using 70 % alcohol and then dried and weighted (Kangur et al., 1998). The collected data on BMI were converted into total biomass.

2.4. Data analyses

The glass eels or elvers restocked in the lake are called "*young of the year*" (YOY) and the eels caught in the commercial fishery – "*yellow eel*". According to the data collected in the last 5 years, the 7 year age group makes up 20 % of the harvest, followed by 8 (17 %) 9 (16 %) and 6 (15 %). 2019 data proved that approximately 56 % of the harvest is FII stage yellow eels, 35 % FIII non migrating silver eels and 8% migrating silver eels (Bernotas and Silm, 2019). To determine the time of the most prominent appearance of the restocked eel in catches, correlations between YOY and *yellow eels* were also calculated shifting the series by 0–12 years relative to each-other. The strongest correlation corresponded to a gap of 7 years (Fig. 1), Therefore, the environmental and feeding conditions 7 years before the catch were considered as those that affected the YOY stage. For *yellow* eels, the environmental parameters from the year of harvest were used, while restocking data was used with a 7-years gap. Statistical analyses were performed using R project 3.5.3 (R Core Team, 2019).

2.5. Variable selection

To detect collinearity among the variables and interactions, Variance Inflation Factor (VIF) was used for testing the presence of the inflated variance of regression coffiencients due to lack of independence between the variables in the model (O'brien, 2007). We used threshold of 8 that, according to literature suggestion, has been considered sufficient to avoid the collinearity (Babak, 2015; Cremona et al., 2018; Feld et al., 2016; Smith et al., 2007) and variables which exceeded this threshold value were excluded from further analyses. In addition, to assess statistical relationship between environmental parameters and eels, Pearson correlation analysis was applied and 'corrplot' used to illustrate the correlation coefficients (Wei and Simko, 2013). Non-parametric regression tool and machine learning method,

Table 2
Restocking/landings year, number of glass eel equivalents (GEE) restocked, number of specimens restocked per hectare of the lake and annual landings of Võrtsjärv commercial fishery.

Year	Restocking (N GEE/sp)	N sp/ha	Landings (kg)
1956	200,000	7.4	ND
1957	0	0.0	ND
1958	0	0.0	ND
1959	0	0.0	ND
1960	60,000	2.2	ND
1961	0	0.0	ND
1962	900,000	33.3	ND
1963	0	0.0	ND
1964	200,000	7.4	3000
1965	700,000	25.9	300
1966	0	0.0	1900
1967	0	0.0	2700
1968	1,400,000	51.9	2900
1969	0	0.0	5000
1970	1,000,000	37.0	6500
1971	0	0.0	6500
1972	100,000	3.7	16,400
1973	0	0.0	21,300
1974	1,800,000	66.7	18,700
1975	0	0.0	36,900
1976	2,600,000	96.3	41,600
1977	2,100,000	77.8	50,000
1978	2,700,000	100.0	45,000
1979	0	0.0	19,000
1980	1,300,000	48.1	17,800
1981	2,700,000	100.0	16,400
1982	3,000,000	111.1	10,800
1983	2,500,000	92.6	24,600
1984	1,800,000	66.7	66,700
1985	2,400,000	88.9	71,900
1986	0	0.0	55,600
1987	2,500,000	92.6	61,200
1988	198,931	7.4	103,700
1989	0	0.0	47,600
1990	0	0.0	56,100
1991	2,000,000	74.1	48,500
1992	2,500,000	92.6	31,000
1993	0	0.0	49,200
1994	1,900,000	70.4	36,900
1995	165,776	6.1	38,800
1996	1,400,000	51.9	34,100
1997	900,000	33.3	40,300
1998	500,000	18.5	21,800
1999	2,300,000	85.2	37,400
2000	1,100,000	40.7	38,800
2001	486,275	18.0	37,600
2002	314,974	11.7	20,400
2003	450,910	16.7	26,400
2004	533,798	19.8	20,100
2005	364,706	13.5	17,600
2006	364,706	13.5	19,900
2007	320,500	11.9	21,500
2008	193,405	7.2	20,500
2009	464,172	17.2	13,600
2010	198,931	7.4	10,300
2011	713,672	26.4	11,300
2012	902,621	33.4	12,600
2013	883,674	32.7	12,700
2014	2,716,850	100.6	13,300
2015	1,600,500	59.3	12,300
2016	1,093,298	40.5	13,000
2017	307,238	11.4	13,800

Random Forests (RF) was performed to select most important parameters for the young of the year and *yellow eels* with 1000trees by using 'package RandomForestSRC' and to estimate the variables importance 'gg_vimp' function was used. (Feld et al., 2016; Ishwaran and Kogalur, 2017).

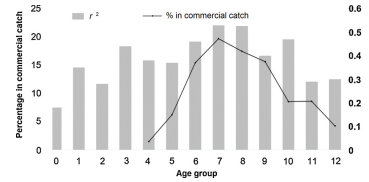

Fig. 1. Bar plot of correlation coefficients of back calculations between yield and number of individual eels restocked (corresponds to the scale on right) and most numerous age groups in the commercial catch (Bernotas and Silm, 2019; corresponds to the scale on left).

2.6. Model construction and selection

Generalized linear models (GLM) were performed for YOY and *yellow* eels with the four predictors which were selected as most important parameters according to RF. Model parameters were centered before GLM, to be eligible for comparison. Interaction and additive effects were tested. Moran's I test was applied on the residuals to test temporal autocorrelation by using the 'ape' package in R (Paradis et al., 2019). The results of Moran I < 0.1 values indicate the absence of significant temporal correlation (Paradis, 2019). Akaike's Information Criterion small-sample equivalent (AICc) was used for evaluation and selection of the model (Akaike, 1973;Brewer et al., 2016). To compare and ordered the models according to AICc values 'dredge' function was applied by using 'MumIn' Package in R (Barton and Barton, 2015). Models were selected among the range of delta AICc (ΔAICc) > 2 that are equally supported (Burnham and Anderson, 2004). R^2 values were considered as goodness of fit of models and model explanatory.

3. Results

3.1. Importance and relationship of selected variables

Significant Pearson correlations for YOY eel (Fig. 2A) were found with total phytoplankton biomass ($r = -0.59$, $p < 0.05$), biomass of cyanobacteria ($r = -0.69$, $p < 0.001$) and summer water temperature ($r = 0.43$, $p < 0.05$), while the commercial yield of *yellow* eels (Fig. 2B) had significant correlations with biomasses of metazooplankton ($r = 0.39$, $p < 0.05$), phytoplankton ($r = -0.36$, $p < 0.05$), cyanobacteria ($r = -0.34$, $p < 0.05$), autumn water temperature ($r = -0.33$, $p < 0.05$) and total phosphorous concentration ($r = 0.38$, $p < 0.05$).

The Random Forest test indicated that the most important parameters during the YOY stage affecting yellow eel density were cyanobacteria biomass, summer water temperature and copepod biomass whereas the number of restocked YOY ranked second after cyanobacteria (Fig. 3). The annual eel harvest rate was most importantly affected by TP (total phosphorus) and metazooplankton in the catching year, and again the restocking numbers 7 years earlier was the second important parameter after TP (Fig. 3).

Food sources during the YOY stage (rotifer, cladoceran, metazooplankton) except for copepods were among the least important parameters determining further eel catch. For *yellow* eels, water physical parameters were least important (secchi, water level, average water temperature). Although, metazooplankton was among the least important parameter for YOY, it was one of the most important parameter for the *yellow* eels.

3.2. Model performance

The GLM model construed for both YOY and *yellow* group of eel

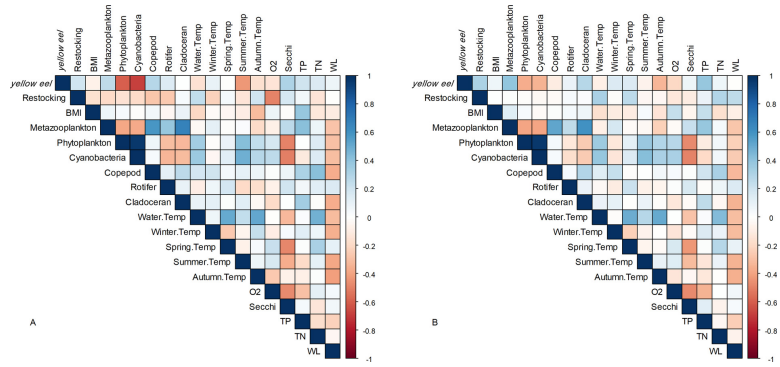

Fig. 2. Pearson correlation of the commercial eel yield with restocking numbers and environmental variables during the YOY stage (7 years before the catch; A) and in the year of catch (*yellow* stage; B). Blue gradients indicate positive correlations and red gradients indicate negative correlations while the intensity of the gradient expresses the correlation strength.

with additive and interaction effects for selected parameters ordered by AIC values is given in Supplementary Table 1. In this study, significant autocorrelation was not detected in any models.

Temporal autocorrelation was detected for neither life stage, and AICc values varied from 68.5–117.7 for YOY eel and from 93.1–124.7 for *yellow* eel. Only ΔAICc < 2 were considered as equally important. Five models were in the range of delta AICc 2 and R^2 varied 0.569 to 0. 0.781 for YOY, while five models were found in the range of delta AICc 2 and R^2 varied from 0.540 to 0.640 for *yellow* eels. Model number 8 and model number 592 were selected because of low df values, stong r^2 and as it took also restocking as a parameter into account. The model outcome revealed that 59 % and 56 % of the variability in YOY and *yellow* eels, respectively, could be explained by the selected parameters that were used in GLM models (Table 1, Fig. 4).

Table 1
Best Generalized Linear Models for eel catches based on restocked number and conditions during YOY and *yellow* stages.

Stage	*Model equation and parameters*	*df*	R^2	*AICc*
YOY	Eel ~ Copepod*(0.357) + Cyanobacteria*(-0.668) + Stocking*(0.170) + ($5.8*10^{-16}$)	5	0.59	69.55
Yellow	Eel ~ Metazooplankton*(0.239) + Stocking *(0.168) + TN*(0.240) + TP*(0.167) + Metazooplankton:TP*(0.295) + TN :TP*(-0.423) – 0.118	8	0.56	94.5

4. Discussion

Our results showed that 59 % of the variability in the YOY survival could be explained by the restocked number and the conditions during

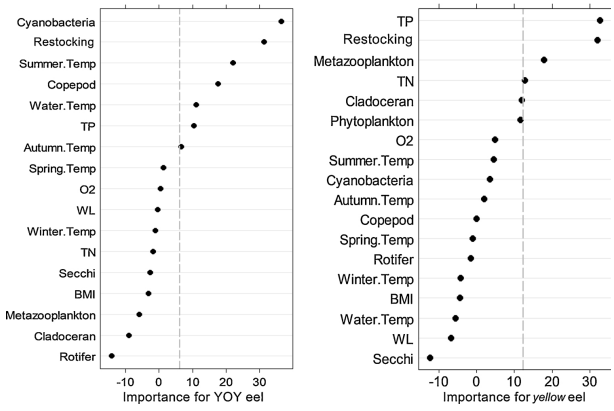

Fig. 3. Dot plots of Random Forest model ranking variables for commercial eel catch by importance: A - during YOY stage (7 years before catch) and B – during *yellow* stage (in the year of catch). Right side of the threshold (vertical dashed line) considered highly important variables for each group, whereas negative and small values are irrelevant for the YOY and *yellow* eels.

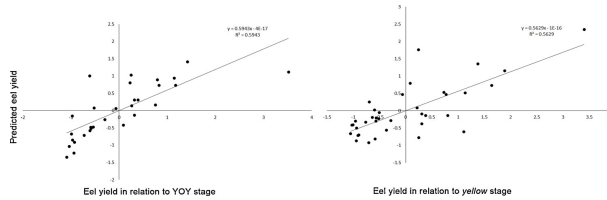

Fig. 4. Centered scatterplots of the predicted eel yield (t) versus eel yield during YOY stage (7 years before catch; t) and eel yield during *yellow* stage (in the year of catch; t). Regression equation and R^2 are provided for each model.

the year of restocking, whereas 56 % of the variability in the harvest rate of the restocked eels by the restocked number and the conditions 7 years later during harvest.

We demonstrated that the number of eels restocked in a given year has a very strong effect on the yield 7 years later highlighting the critical importance of growth conditions during the first lake year for the glass eels. While being introduced to a water body, eels sustain extra stress making them more vulnerable to environmental stressors. It has been suggested that early life-history stages of fish are most affected by environmental changes (Rijnsdorp et al., 2009). Presumably glass eels are subject to vast mortality during the first few months after recruitment (Lambert, 2008). Also, handling during restocking activities (Josset et al., 2015) and predator attacks directly after restocking (Ovidio et al., 2015) could affect the glass eel mortality. In the context of Võrtsjärv, gulls (*Laridae*) have been observed to prey on glass eel while restocking has taken place during daylight (*Unpublished observation, P.B.*). Glass eels were also discovered in the stomachs of perch right after restocking activities on Võrtsjärv (*Unpublished data, P.B.*). Unfortunately, we could not add predation as a factor into the model due to lack of data available.

Our results showed that the prevalence of cyanobacteria in the water body has the strongest negative effect on YOY. Restocking of eels in Võrtsjärv takes usually place in spring when cyanobacterial populations are starting to grow and their abundance is still low. However, rapid growth of cyanobacteria in early summer results in peak of cyanobacterial biomass in mid-summer (Nõges et al., 2004). Observations have shown that when glass eels are introduced to a water body, they prefer shallow sheltered habitats where water movement is low (Ovidio et al., 2015). In a context of a large lake, this counts for littoral areas where cyanobacterial scum formations or benthic populations are known to form (Malbrouck and Kestemont, 2006). The period of time necessary for restocked eels to recover from stress associated with transport and introduction to a water body is not known neither is the time it takes for restocked eels to start feeding. So during the first lake year, glass eels grow side by side with the increase of cyanobacterial populations which means the latter can have an effect on the growth of restocked glass eels. A study by (Engström-Öst and Isaksson, 2006) showed that the feeding of pike larvae decreased in the presence of cyanobacteria. It could very well be that filamentous cyanobacterial formations have similar effect on the behavior of glass eels. Glass eels may feed on various food sources in fresh water habitats. A study carried out by (Belpaire et al., 1992) indicated that in freshwater ponds the most important prey for glass eels were Cladocera and Ceratopogonidae. Both these taxa are also very common in the littoral zone of Võrtsjärv (Kangur et al., 2004; Nõges et al., 2004), making them theoretically a preferred food source for restocked glass eels. It is known that abundance of cladocerans can be affected negatively by the formation of cyanobacterial blooms or by the rise of cyanobacterial biomass in the lake (Ghadouani et al., 2003; Gliwicz, 1990). Also, through increasing the complexity of a habitat, filamentous algae have a negative influence on the foraging success of juvenile fish (Pihl et al., 1995). Similar negative influence from cyanobacteria has been observed with BMI (Krivosheina, 2008). Our results showed that neither cladoceran abundance nor BMI impacted restocked glass eels significantly. However lower feeding success of fish larvae (such as glass eels) can depend on lower visibility (Utne-Palm, 2002) or clogging of the gills during cyanobacterial blooms (Engström-Öst and Isaksson, 2006). So years with unfavourable environmental conditions (such as cyanobacterial prevalence) during restocking year have a stronger effect on the yield than just smaller number of restocked individuals.

The “copepod” effect could be interpreted through copepods being an intermediate host for swim bladder parasite *Anguillicola Crassus* (Hubbard et al., 2016; Kirk, 2003). It has been found that crustaceans serve as intermediate parasite hosts for smaller (< 20 cm) eels; (Thomas and Ollevier, 1992) and glass eels might be infected as soon as they start feeding (Nimeth et al., 2000). Surprisingly it has been found that infected eels can have greater body length and mass compared to uninfected specimens (Lefebvre et al., 2013). The aforementioned study also hypothesizes that as actively foraging individuals are more likely to get infected they are also more likely to get caught by passive fishing gear (Lefebvre et al., 2013). In Võrtsjärv 49 % of the legal sized eels are known to be infected with *A. Crassus* (Bernotas and Silm, 2019). So during years with high copepod biomass, restocked glass eels may have an increased consumption of copepods which over our studied 7 year cycle has a positive effect on the yield but also reflects in the high ratio of infected eels in the population.

Effectiveness of fishery can be described by catchability which is a combined result of fish abundance and fishing effort (Arreguín-Sánchez, 1996). Thus, it could be assumed that at a constant fishing effort, catchability be defined by fish abundance. However, environmental parameters and fish behavior also influence the catchability (Hilborn and Walters, 2013; Hubert and Pope, 2012; Rogers et al., 2003). Our results indicated that some environmental factors during the fishing year have significant influence on the commercial yield of eel. Most notably, TP concentration in the fishing year had the strongest effect on *yellow* eel harvest. High TP concentrations in water give evidence of eutrophication and thus can be related to low fish diversity (Naigaga et al., 2011), higher abundance of cyprinids such as Common carp (*Cyprinus carpio)* (Carol et al., 2006) a decline in piscivores (Du et al., 2015) or a decrease in *Anguilla* spp. catch and abundance (Rönnberg and Bonsdorff, 2004; Thomas et al., 1993). However, in case of eel, our results were opposite. Instead of decreasing yield during the years with high TP concentrations, it increased. This could be explained with the nature of the local fishery. Only fyke nets are used for catching eel on Võrtsjärv. When fishing with passive gear, first the fish must encounter the gear (Hubert and Pope, 2012). This means that the commercial yield in Võrtsjärv is directly connected to fish movement that may be stimulated by high TP concentrations. One plausible explanation could be that during years with high TP concentrations in the water, benthic habitats become inhabitable during high growth periods because of hypoxia (Correll, 1998) making eels leave their habitat in search for more suitable conditions. Still the exact reason behind the rise in eel

catch during high TP concentrations in Võrtsjärv needs to be studied further.

The immediate positive effect of metazooplankton abundance on the *yellow* eel stock may reflect a decline in planktivorous fish and their relationship to diet changes of benthivorous fish. Bream, roach (*Rutilus rutilus*) and perch are all abundant species in Võrtsjärv (Järvalt, 2003). It was found that with a decrease in planktivorous fish biomass, changes in the diet of bream (TL < 300 mm), roach (larger size classes) and perch (TL = 120 − 150 mm) were observed (Persson and Hansson, 1999). All of the aforementioned groups had a tendency to switch from pelagic to benthic prey when planktivorous fish communities were altered (Persson and Hansson, 1999). In Võrtsjärv macroinvertebrates are a preferred food source for eels (Kangur et al., 1999; Teesalu, 2019), and they adapt their diet to the most available food source (Bouchereau et al., 2009). Increased food competition from other species may increase the migrations of eels within a water body however whether such migrations increase the possibility of being caught by passive fishing gear needs to be addressed in future studies.

Interactions of environmental factors such as TP with metazooplankton and TN with TP during the harvest year may also affect the yellow eel harvest rate. While the positive impact of the TP and metazooplankton interaction can be explained by the effects discussed in the preceding two paragraphs, the negative influence of TN:TP interaction can also be connected to the TP concentration. Higher TN:TP values relate to oligotrophic lakes which obtain the N and P from undisturbed sources that export less P than N while lower TN:TP values are connected with meso- or eutrophic water bodies (Downing and McCauley, 1992). High TN:TP ratio means smaller TP concentration in the water body which in turn has a negative effect on the yellow eel harvest rate.

4.1. Study limitations

Although data on restocking densities is hard to find we assumed for this study the restocking densities in Võrtsjärv to be low. The average number of GEE restocked per hectare during the study period was 33 specimens (Table 2). Assuming a mean weight of a specimen being 0.3 g this means a restocking density of 0.00099 g per m^2. As natural mortality of restocked glass eels or elvers is very difficult to observe in the wild we assumed a constant annual rate of M = 0.1. Due to lack of data from most of the study period assumption on a constant growth rate was also made.

5. Conclusion

Based on the results of our study it can be concluded that environmental conditions in a water body during the time of restocking play an important role in determining the future yields of eel. It was concluded that during the year of the harvest, environmental factors affected the yield to a lesser extent. Although we concentrated on predicting the impact on commercial yield, in conditions of a steady fishing effort like in Võrtsjärv where the number of fishing gear has remained constant, the yield could very well represent also eel biomass. The parameters most affecting restocked eels vary likely between different water bodies but in case of eutrophic lakes, the leading factors described in the present study should be studied further to optimize future eel restockings. Also if there is a choice between different water bodies where to restock eels and if data is available it would be recommended to take the relationships discussed in this study into consideration to account for either a positive or negative effect on the restocked eel population.

CRediT authorship contribution statement

Priit Bernotas: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Burak Öğlü:** Conceptualization, Methodology, Software, Writing - original draft, Visualization. **Peeter Nõges:** Writing - original draft, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2020.105649.

References

Akaike, H., 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika 60 (2), 255–265.
Anneville, O., Domaizon, I., Kerimoglu, O., Rimet, F., Jacquet, S., 2015. Lakes as sentinels of climate change. Ecosystems 18, 2283–2297. https://doi.org/10.4319/lo.2000.45.3.0591.
Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. Rev. Fish Biol. Fish. 6, 221–242. https://doi.org/10.1007/bf00182344.
Babak, N., 2015. Uncertainty Analysis for Species Distribution Models. R Packag. Version 1.1 15.
Barton, K., Barton, M.K., 2015. Package ‘MuMIn.’ Version 1, 18.
Belpaire, C., Van Driessche, H., Gao, F.Y., Ollevier, F., 1992. Food and feeding activity of glass eel Anguilla anguilla (L.) stocked in earthen ponds. Irish Fish. Investig. Ser. A Freshw 36, 43–54.
Bernotas, P., Silm, M., 2019. Report on the eel stock, fishery and other impacts, in Estonia. ICES. 2019. Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL). ICES Scientific Reports. 1:50. https://doi.org/10.17895/ices.pub.5545. 177 pp.
Bernotas, P., Vetemaa, M., Saks, L., Eschbaum, R., Verliin, A., Järvalt, A., 2016. Dynamics of European eel landings and stocks in the coastal waters of Estonia. ICES J. Mar. Sci. J. du Cons. 73, 84–90. https://doi.org/10.1093/icesjms/fsv245.
Bernotas, P., Silm, M., Järvalt, A., 2018. Report on the eel stock, fishery and other impacts. In: Estonia 2018. ICES, 2018. Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL) 5-12 September 2018. Gdansk, Poland. ICES CM 2018/ACOM:15 152.
Bouchereau, J.L., Marques, C., Pereira, P., Guélorget, O., Vergne, Y., 2009. Food of the European eel Anguilla anguilla in the Mauguio lagoon (Mediterranean, France). Acta Adriat. 50, 159–170.
Brewer, M.J., Butler, A., Cooksley, S.L., 2016. The relative performance of AIC, AICC and BIC in the presence of unobserved heterogeneity. Methods Ecol. Evol. 7, 679–692. https://doi.org/10.1111/2041-210X.12541.
Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. https://doi.org/10.1177/0049124104268644.
Carol, J., Benejam, L., Alcaraz, C., Vila-Gispert, A., Zamora, L., Navarro, E., Armengol, J., García-Berthou, E., 2006. The effects of limnological features on fish assemblages of 14 Spanish reservoirs. Ecol. Freshw. Fish 15, 66–77. https://doi.org/10.1111/j.1600-0633.2005.00123.x.
Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R., Brock, W.A., Cline, T., Coloso, J., Hodgson, J.R., Kitchell, J.F., Seekell, D.A., Smith, L., Weidel, B., 2011. Early warnings of regime shifts: a whole-ecosystem experiment. Science 332 (80), 1079–1082. https://doi.org/10.1126/science.1203672.
Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Modell. 172, 109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003.
Correll, D.L., 1998. Role of phosphorus in the eutrophication of receiving waters: a review. The correl.pdf. J.Enviro. Quall 261–266.
Cremona, F., Tuvikene, L., Haberman, J., Nõges, P., Nõges, T., 2018. Factors controlling the three-decade long rise in cyanobacteria biomass in a eutrophic shallow lake. Sci. Total Environ. 621, 352–359. https://doi.org/10.1016/j.scitotenv.2017.11.250.
Dekker, W., 2015. Aqua Reports 2015: 11 Assessment of the Eel Stock the Swedish Eel Management Plan.
Dekker, W., 2016. Management of the eel is slipping through our hands! Distribute control and orchestrate national protection. ICES J. Mar. Sci. J. du Cons. fsw094. https://doi.org/10.1093/icesjms/fsw094.

Dekker, W., Beaulaton, L., 2016. Faire mieux que la nature? The history of eel restocking in Europe. Environ. Hist. 22, 255–300. https://doi.org/10.3197/096734016X14574329314407.

Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr. Mar. Biol. an Annu. Rev. 33, 245–303.

Downing, J.A., McCauley, E., 1992. The nitrogen: phosphorus relationship in lakes. Limnol. Oceanogr. 37 (5), 936–945.

Drouineau, H., Durif, C., Castonguay, M., Mateo, M., Rochard, E., Verreault, G., Yokouchi, K., Lambert, P., 2018. Freshwater Eels : a Symbol of the Effects of Global Change. pp. 903–930. https://doi.org/10.1111/faf.12300.

Du, X., García-Berthou, E., Wang, Q., Liu, J., Zhang, T., Li, Z., 2015. Analyzing the importance of top-down and bottom-up controls in food webs of Chinese lakes through structural equation modeling. Aquat. Microb. Ecol. 49, 199–210. https://doi.org/10.1007/s10452-015-9518-3.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. Biol. Rev. Camb. Philos. Soc. 81, 163–182. https://doi.org/10.1017/S1464793105006950.

Engström-Öst, J., Isaksson, I., 2006. Effects of macroalgal exudates and oxygen deficiency on survival and behaviour of fish larvae. J. Exp. Mar. Bio. Ecol 335, 227–234. https://doi.org/10.1016/j.jembe.2006.03.007.

Feld, C.K., Segurado, P., Gutiérrez-Cánovas, C., 2016. Analysing the impact of multiple stressors in aquatic biomonitoring data. A 'cookbook' with applications in R. Sci. Total Environ 573, 1320–1339. https://doi.org/10.1016/j.scitotenv.2016.06.243.

Ficke, A.D., Myrick, C.A., Hansen, L.J., 2007. Potential impacts of global climate change on freshwater fisheries. Rev. Fish Biol. Fish. https://doi.org/10.1007/s11160-007-9059-5.

Ghadouani, A., Pinel-Alloul, B., Prepas, E.E., 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. Freshw. Biol. 48, 363–381. https://doi.org/10.1046/j.1365-2427.2003.01010.x.

Gliwicz, Z.M., 1990. Why do cladocerans fail to control algal blooms? Hydrobiologia 200–201, 83–97. https://doi.org/10.1007/BF02530331.

Hecky, R.E., Mugidde, R., Ramlal, P.S., Talbot, M.R., Kling, G.W., 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. Freshw. Biol. 55, 19–42. https://doi.org/10.1111/j.1365-2427.2009.02374.x.

Hilborn, R., Walters, C.J., 2013. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Springer Science Business Media.

Hubbard, I.M., Hill-Spanik, K.M., Knott, D., Buron, Ide, 2016. Development of anguillicoloides crassus in a cyclopoid copepod from the Acanthocyclops robustus–americanus–vernalis complex in South Carolina, U.S.A. Comp. Parasitol. 83, 192–196. https://doi.org/10.1654/4835sed.1.

Hubert, W.A., Pope, K.L., 2012. DigitalCommons @ University of Nebraska - Lincoln Passive Capture Techniques Chapter 6 Passive Capture Techniques.

Ishwaran, H., Kogalur, U.B., 2017. Random Forests for Survival, Regression and Classification (RF-SRC), R Package Version 1.6. Available at: http://www.ccs.miami.edu/~hishwaran/ishwaran.html. .

Janatian, N., Olli, K., Cremona, F., Laas, A., Nõges, P., 2019. Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake. Limnol. Oceanogr. 65 (2020), 717–731.

Järvalt, A., 2003. Fishes and fishery of võrtsjärv. Lake Võrtsjärv 335–354.

Järvet, A., 2004. Hydrology of lake võrtsjärv. Lake Võrtsjärv 105–139.

Josset, Q., Trancart, T., Mazel, V., Charrier, F., Frotté, L., Acou, A., Feunteun, E., 2015. Pre-release processes influencing short-term mortality of glass eels in the French eel (Anguilla anguilla, Linnaeus 1758) stocking programme. ICES J. Mar. Sci. 73, 150–157. https://doi.org/10.1093/icesjms/fsv074.

Kangur, K., Timm, H., Timm, T., Timm, V., 1998. Long-term changes in the macrozoobenthos of Lake Võrtsjärv. Limnologica 28, 75–83.

Kangur, K., Kangur, A., Kangur, P., 1999. A comparative study on the feeding of eel, Anguilla anguilla (L.), bream, Abramis brama (L.) and ruffe, Gymnocephalus cernuus (L.) in Lake Võrtsjärv, Estonia. Shallow Lakes' 98. Springer, pp. 65–72.

Kangur, K., Timm, H., Timm, T., 2004. Zoobenthos. Lake Võrtsjärv. pp. 265–280.

Kirk, R.S., 2003. The impact of Anguillicola crassus on European eels. Fish. Manag. Ecol. 10, 385–394. https://doi.org/10.1111/j.1365-2400.2003.00355.x.

Krivosheina, M.G., 2008. On insect feeding on cyanobacteria. Paleontol. J. 42, 596–599. https://doi.org/10.1134/S003103010806004X.

Laffaille, P., 2003. Spatial Organisation of European Eel. https://doi.org/10.1046/j.1600-0633.2003.00021.x.

Lambert, P., 2008. Evaluation Des Effets Possibles De Différents Niveaux De Réduction Des Impacts Anthropiques Sur Le Temps De Restauration Du Stock d'anguille Européenne. Rapp. CEMAGREF/ONEMA 22 p.

Lefebvre, F., Fazio, G., Mounaix, B., Crivelli, A.J., 2013. Is the continental life of the European eel Anguilla anguilla affected by the parasitic invader Anguillicoloides crassus? Proc. R. Soc. B Biol. Sci 280. https://doi.org/10.1098/rspb.2012.2916.

Malbrouck, C., Kestemont, P., 2006. Effects of microcystins on fish. Environ. Toxicol. Chem. 25, 72–86. https://doi.org/10.1897/05-029R.1.

Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fish. Res. 142, 86–99. https://doi.org/10.1016/j.fishres.2012.10.012.

Mooij, W.M., Hu, S., Domis, L.N.D.S., Bart, A., 2005. The Impact of Climate Change on Lakes in the Netherlands: a Review the Impact of Climate Change on Lakes in the Netherlands: a Review. https://doi.org/10.1007/s10452-005-9008-0.

Mugidde, R., Hecky, R.E., Hendzel, L.L., Taylor, W.D., 2003. Pelagic nitrogen fixation in Lake Victoria (East Africa). J. Great Lakes Res. 29, 76–88. https://doi.org/10.1016/S0380-1330(03)70540-1.

Naigaga, I., Kaiser, H., Muller, W.J., Ojok, L., Mbabazi, D., Magezi, G., Muhumuza, E., 2011. Fish as bioindicators in aquatic environmental pollution assessment: a case study in Lake Victoria wetlands. Uganda. Phys. Chem. Earth 36, 918–928. https://doi.org/10.1016/j.pce.2011.07.066.

Nimeth, K., Zwerger, P., Würtz, J., Salvenmoser, W., Pelster, B., 2000. Infection of the glass-eel swimbladder with the nematode Anguillicola crassus. Parasitology 121, 75–83. https://doi.org/10.1017/S003118209900606X.

Nõges, P., Nõges, T., 2014. Weak trends in ice phenology of Estonian large lakes despite significant warming trends. Hydrobiologia 731 (1), 5–18.

Nõges, P., Laugaste, R., Nõges, T., 2004. Phytolankton. In: Haberman, J., Pihu, E. (Eds.), Lake Vortsjärv. Estonian Encyclopaedia Publishers, Tallinn. Estonian Encyclopaedia Publishers, Tallinn, pp. 217–231.

Nõges, T., Arst, H., Laas, A., Kauer, T., Nõges, P., Toming, K., 2011. Reconstructed long-term time series of phytoplankton primary production of a large shallow temperate lake: the basis to assess the carbon balance and its climate sensitivity. Hydrobiologia 667 (1), 205–222.

Nõges, T., Anneville, O., Guillard, J., Haberman, J., Järvalt, A., Manca, M., Morabito, G., Rogora, M., Thackeray, S.J., Volta, P., Winfield, I.J., Nõges, P., 2018. Fisheries impacts on lake ecosystem structure in the context of a changing climate and trophic state. J. Limnol. 77, 46–61. https://doi.org/10.4081/jlimnol.2017.1640.

O'Brien, R.M., 2007. A caution regarding rules of thumb for variance inflation factors. Qual. Quant. 41, 673–690. https://doi.org/10.1007/s11135-006-9018-6.

Öğlü, B., Bhele, U., Järvalt, A., Tuvikene, L., Timm, H., Seller, S., Haberman, J., Agasild, H., Nõges, P., Silm, M., Bernotas, P., Nõges, T., Cremona, F., 2019. Is fish biomass controlled by abiotic or biotic factors? Results of long-term monitoring in a large eutrophic lake. J. Great Lakes Res. https://doi.org/10.1016/j.jglr.2019.08.004.

Ovidio, M., Tarrago-Bes, F., Matondo, B.N., 2015. Short-term responses of glass eels transported from UK to small Belgian streams. Annales de Limnologie-Int. J. Limnol. 219–226.

Paerl, H.W., Huisman, J., 2008. Climate: blooms like it hot. Science 320 (80), 57–58. https://doi.org/10.1126/science.1155398.

Paerl, H.W., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1, 27–37. https://doi.org/10.1111/j.1758-2229.2008.00004.x.

Paradis, E., 2019. Moran's Autocorrelation Coefficient in Comparative Methods.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H.S., Desper, R., 2019. Package 'ape.' Anal. phylogenetics EvoVersion 2.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 697–706. https://doi.org/10.1006/jmsc.2000.0726.

Persson, A., Hansson, L.A., 1999. Diet shift in fish following competitive release. Can. J. Fish. Aquat. Sci. 56, 70–78. https://doi.org/10.1139/f98-141.

Pihl, L., Isaksson, I., Wennhage, H., Moksnes, P.O., 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. Netherlands J. Aquat. Ecol. 29, 349–358. https://doi.org/10.1007/BF02084234.

Pihu, E., 1998. Fishes and fisheries management in Lake Võrtsjärv. Limnologica 28, 91–94.

Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J. Fish Biol. 77, 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x.

R Core Team, 2019. A Language and Environment for Statistical Computing. R Found. Stat. Comput.

Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C., Pinnegar, J.K., 2009. Resolving the effect of climate change on fish populations. ICES J. Mar. Sci. 66, 1570–1583. https://doi.org/10.1093/icesjms/fsp056.

Rogers, M.W., Hansen, M.J., Beard, T.D., 2003. Catchability of walleyes to Fyke Netting and Electrofishing in Northern Wisconsin Lakes. North Am. J. Fish. Manag. 23, 1193–1206. https://doi.org/10.1577/m02-121.

Rönnberg, C., Bonsdorff, E., 2004. Baltic Sea eutrophication: area-specific ecological consequences. Hydrobiologia 514, 227–241. https://doi.org/10.1023/B:HYDR.0000019238.84989.7f.

Smith, G.M., Zuur, A., Ieno, E.N., 2007. Analysing ecological data.

Teesalu, P., 2019. The Role of trophic niche in eel head shape dimorphism. Eesti Maaülikool.

Tesch, F.W., Bartsch, P., Berg, R., Gabriel, O., Henderson, I.W., Kamstra, A., Kloppmann, M., Reimer, L.W., Wirth, T., White, R.J., Thorpe, J.E., 2003. The Eel.

Thomas, K., Ollevier, F., 1992. Paratenic hosts of the swimbladder nematode Anguillicola crassus. Dis. Aquat. Organ. 13, 165–174. https://doi.org/10.3354/dao013165.

Thomas, G.H., el-Karyony, I.A., Hassan, A.H., 1993. Phosphorus-nitrogen loading and trend of fish catch as index of lake Mariut eutrophication. J. Egypt. Public Health Assoc. 68, 593–615.

Thorson, J.T., 2019. Predicting recruitment density dependence and intrinsic growth rate for all fishes worldwide using a data-integrated life-history model. Fish Fish. Oxf. (Oxf) 1–15. https://doi.org/10.1111/faf.12427. in press.

Tõnno, I., Agasild, H., Kõiv, T., Freiberg, R., Nõges, P., Nõges, T., 2016. Algal diet of small-bodied crustacean zooplankton in a cyanobacteria-dominated eutrophic lake. PLoS One 11, 1–17. https://doi.org/10.1371/journal.pone.0154526.

Tuvikene, L., Nõges, T., Nõges, P., 2011. Why do phytoplankton species composition and "traditional" water quality parameters indicate different ecological status of a large shallow lake? Hydrobiologia 660 (1), 3–15.

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar. Freshw. Behav. Physiol. 35, 111–128. https://doi.org/10.1080/10236240290025644.

Wei, T., Simko, V., 2013. Corrplot: Visualization of a Correlation Matrix. R Packag. Version 0.73 230. pp. 11.

Woodward, G., Perkins, Daniel M.ichael, Brown, Lee E., 2010. Climate Change and Freshwater Ecosystems : Impacts Across Multiple Levels of Organisation. https://doi.org/10.1098/rstb.2010.0055.

IV

Tambets, M., Kärgenberg, E., Järvalt, A., Økland, F., Kristensen, M. L., Koed, A., & **Bernotas, P.** (2021). Migrating silver eels return from the sea to the river of origin after a false start. *Biology Letters, 17*(9), 20210346.

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Animal behaviour

Migrating silver eels return from the sea to the river of origin after a false start

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The European eel's singular spawning migration from European waters towards the Sargasso Sea remains elusive, including the early phase of migration at sea. During spawning migration, the movement of freshwater resident eels from river to sea has been thought to be irreversible. We report the first recorded incidents of eels returning to the river of origin after spending up to a year in the marine environment. After migrating to the Baltic Sea, 21% of the silver eels, tagged with acoustic transmitters, returned to the Narva River. Half returned 11–12 months after moving to the sea, with 15 km being the longest upstream movement. The returned eels spent up to 33 days in the river and migrated to the sea again. The fastest specimen migrated to the outlet of the Baltic Sea in 68 days after the second start—roughly 1300 km. The surprising occurrence of returning migrants has implications for sustainable management and protection of this critically endangered species.

1. Introduction

The European eel *Anguilla anguilla* (L., 1758) stands out among other fish species by its unique spawning migration. The route from European waters to the Sargasso Sea, its likely spawning ground, stretches from 5000 to 10 000 km, which is the longest distance among anguillid eels [1–3]. Eels are semelparous, meaning they have a chance to spawn only once in a lifetime. The realization of reproductive potential for which eels have invested much energy and time (approximately 10 to 20, even 44 years; [4,5]) is determined by the success of a long and dangerous spawning migration [3].

European eel stocks have collapsed in recent decades; juvenile eel abundance has decreased by over 90% [6]. The species is considered critically endangered [7]. Their decline is associated with the drastic negative effect of habitat loss, hydropower, overfishing, climate change, pollution, parasites and diseases on spawning stock size [7,8]. Eel spawning stock is determined by the number of migrating silver eels (escapement) from the waters of North Africa to the northern tip of Scandinavia [9,10]. In the first decade of the 2000s, European Union countries established a common eel-recovery strategy [11]. The main recovery measure is increasing the escapement of silver eel biomass to at least 40%, relative to the best estimate of escapement that existed before anthropogenic impacts to the stock. In addition to the number or biomass of escaping silver eels, the size of the spawning stock depends on the success of silver eel spawning migration, which is also important when planning appropriate conservation measures for the species.

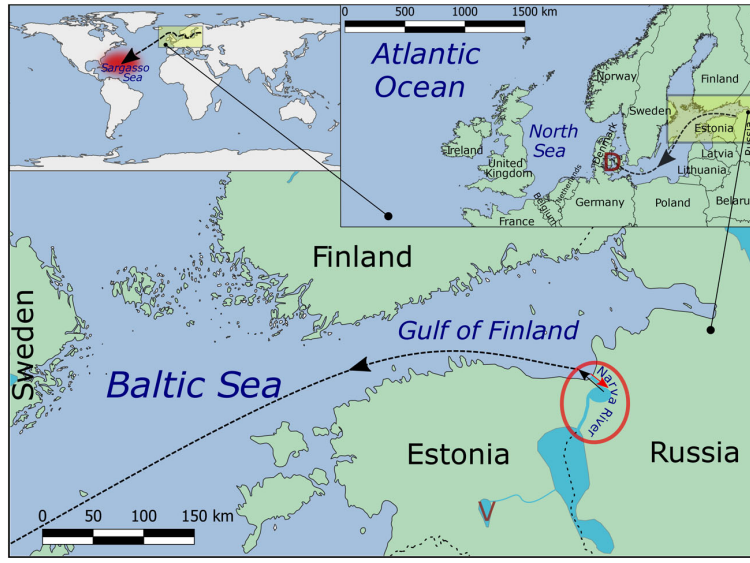

Figure 1. Study area. European eel migration from freshwater areas towards spawning areas in the Sargasso Sea (dashed line on top left) was studied with acoustic telemetry during its first quarter of migration (dashed line on top right). Acoustic receivers were located in Danish Straits (D), Narva reservoir and the Narva River (red ellipse bottom right). The experimental fish were caught in Lake Võrtsjärv (V).

Many studies indicate that the success of spawning migration depends on the route and timing of migration ([12] and references therein). The right timing assures that in every phase of the migration, eels are in suitable physical condition, environmental factors (water temperature, currents, salinity, etc.) are favourable and the predation risk is minimal [4]. Failures in migration timing, including delays caused by man-made obstacles, can be costly [8]. It has been shown that the timing of migration is adjusted according to the conditions in freshwaters, estuaries and marine waters [12–16].

Eels that have migrated to the sea from freshwater might not start swimming directly towards the Sargasso Sea. Recent findings suggest that silver eels, after descent to saltwater, may remain temporarily in coastal areas or fjords, thereby performing a two-step migration [12,13,17–20]. Such an extended residence prior to seaward migration appears to be characteristic not only for the European eel but also for other species, such as *Anguilla australis* and *Anguilla rostrata* [12,21]. This halt might even continue for years [22,23], resulting in considerable delay in the spawning migration of eels. The effects of such delays during spawning migration on successful passage to the Sargasso Sea are unclear (see e.g. [17,24,25]). It is demonstrated that eels can also stop or make temporary upstream movements inside an estuarine habitat [14]. However, return from the sea to a freshwater part of a river by silver eels has not previously been scientifically documented.

In the context of the Baltic Sea, silver eels migrating towards the Atlantic Ocean may cover the distance from the Narva River to the ocean, i.e. Danish Straits (approx. 1300 km) in five months; however, the journey often lasts longer [26], implying a pause in migration. Although fish can theoretically stop or rest at any point along with this phase of migration, presumably it might occur near the river mouth. This study was initially designed with a focus on the downstream migration of eels and an exit from the Baltic Sea during an extended time period. Using tags with an extended operating lifetime made it possible to detect the phenomenon of eel return from the sea to the river. The present paper sought to improve comprehension of silver eel migration between the river and the sea and to see whether any delays in migration or unseen patterns of movements from one environment to another exist during two main migration seasons.

2. Methods

(a) Study area

To study silver eels' behaviour, fish were tracked in riverine and marine environments during their migration from the Narva River reservoir towards an outlet of the Baltic Sea to the North Sea. The Narva River discharges (400 $m^3 s^{-1}$) to the Gulf of Finland in the Baltic Sea (figure 1). The Baltic is a brackish sea with a limited connection to the open ocean and its salinity is controlled by freshwater outflow from rivers and inflow of saline waters from the North Sea [27]. The salinity of the Baltic Sea decreases along with a notional line from west (Kattegat) to east (Gulf of

Table 1. Environmental data during the first migration of the European eel from the Narva River to the Baltic Sea (ordered by the date of the first descent). Fish returning to the river after descending to the sea are in bold. The significance of environmental predictors for the probability of eel return was assessed using the LRT. The water temperatures and discharges during fish entering the sea are based on daily averages of River Narva. Moon phase during entering the sea is expressed as moon illumination rate (at New Moon and Full Moon the per cent illuminated is 0 and 100%, respectively). Dates of leaving the Narva Reservoir and reaching the Danish Straits are provided. * represents the fish caught in the sea *ca* 50 km northeast from the river mouth on 20 October 2019.

Eel ID	date entering the sea	date leaving the Narva Reservoir	temperature (°C)	discharge ($m^3\ s^{-1}$)	moon phase (%)	date reaching the Danish Straits
166	25.10.18	24.10.18	8.2	412	99	
179	″	″	″	″	″	
183	″	″	″	″	″	
188	″	″	″	″	″	
176	″	25.10.18	″	″	″	
182	26.10.18	24.10.18	7.7	334	96	
189	″	25.10.18	″	″	″	
193	27.10.18	26.10.18	7.3	316	91	
200	″	24.10.18	″	″	″	
208	″	25.10.18	″	″	″	30.09.19
162	28.10.18	27.10.18	6.5	317	84	
173	″	**26.10.18**	″	″	″	**06.02.20**
181	″	27.10.18	″	″	″	
192	″	28.10.18	″	″	″	
206	″	25.10.18	″	″	″	
184	31.10.18	30.10.18	4	307	53	02.12.19
172	**04.11.18**	**03.11.18**	**5.4**	**463**	**13**	
168	05.11.18	04.11.18	5.4	456	6	
191	″	**04.11.18**	″	″	″	
190	10.11.18	09.11.18	6.1	358	8	
201	**11.11.18**	**11.11.18**	**5.7**	**357**	**14**	
163	**12.11.18**	″	**5.5**	**369**	**22**	**30.12.19**
171	″	″	″	″	″	
174	″	″	″	″	″	
178	″	″	″	″	″	
198	″	″	″	″	″	
177	13.11.18	12.11.18	5	413	30	
197	″	″	″	″	″	11.12.19
195*	″	13.11.18	″	″	″	
212	14.11.18	11.11.18	4.9	437	39	
213	19.11.18	12.11.18	4.6	449	84	
167	05.05.19	27.04.19	8.3	437	0	21.11.19
161	**27.05.19**	**22.04.19**	**15.2**	**229**	**43**	**19.01.20**
209	15.06.19	30.04.19	19.5	394	96	15.02.20
175	20.06.19	12.05.19	21.4	425	91	
205	**30.06.19**	**18.04.19**	**19.3**	**449**	**7**	
164	25.09.19	20.04.19	10.4	311	16	
196	23.10.19	28.10.18	8.7	296	29	
average values for the returners (mean)	**29.12.18**		**8.9**	**382**	**36**	**18.01.2020**
average values for the rest fish (mean)	16.12.18		7.5	368	60	04.12.2019

(*Continued*.)

Table 1. (*Continued.*)

Eel ID	date entering the sea	date leaving the Narva Reservoir	temperature (°C)	discharge ($m^3\ s^{-1}$)	moon phase (%)	date reaching the Danish Straits
statistics of LRT	χ^2		0.64	0.37	2.79	
	d.f.		1	1	1	
	P		0.42	0.54	0.10	

Finland) with the mean value of 6‰ [28]. The average depth of the Baltic Sea and the Gulf of Finland area is 55 m and 38 m, respectively. The distance from the Narva River mouth to the Danish Straits is approximately 1300 km.

(b) Fish, tagging and tracking

An acoustic telemetry method was used to track the movements of 38 silver eels migrating to and through the Baltic Sea from the Narva River. The experimental fish were caught in Lake Võrtsjärv, situated in the Narva River catchment area, *ca* 250 km from the sea. The eels in the lake are all restocked as glass eels or elvers. The tagged fish were of silvering appearance with a length of 604 to 896 mm (mean total length ± s.d.: 700 ± 78 mm), a weight of 371 to 1495 g (mean total weight ± s.d.: 680 ± 261 g), and with silvering stages of FIII to FV ([29]; electronic supplementary material, table S1). Before tagging, the eels were anaesthetized in an aqueous solution of metomidate (40 mg l^{-1}; Aquacalm, Syndel Laboratories Ltd., Canada). Coded acoustic transmitters 9 × 27.5 mm (d × l) were surgically implanted into the body cavities (Vemco, Nova Scotia, Canada, V9-2 L-A69-1602 tags, with a random pulse delay of 40–80 s, 476 days). Eels were released into the Narva River reservoir (water temperature 8.5°C), 20 km from the river mouth on 24 October 2018. The fish were transported by car in 1 m^3 aerated tanks.

In the river and reservoir, the fish were monitored by eight stationary Vemco VR2 W automatic receivers (electronic supplementary material, figure S1). To confirm the descent of the eels from the river to the sea, manual tracking (Vemco VR100) was performed nine times in the 5 km long river mouth area.

A total of 45 acoustic receivers were deployed in the Danish Straits during August and September 2019 (electronic supplementary material, figure S2). The receivers covered all three natural exits from the Baltic Sea to the Kattegat/North Sea. Receivers were mounted on bridges ($N = 35$) or with Desert Star ARC-1XD acoustic release systems on the sea floor ($N = 10$). Receivers mounted on bridges and, on sea floor moornings, were deployed with a distance of 410–440 and 300–550 m between receivers, respectively. Due to severe storms in November to December 2019, one natural exit was covered partially.

(c) Data analysis

Statistical tests were performed using the program R v. 4.0.2 [30].

The Clopper–Pearson method was used to calculate the binomial 95% confidence interval (CI) for the point estimate of the proportion of returning eels.

The probability of tagged eels returning to the river from the sea was calculated by logistic regression models, with biological fish parameters and environmental parameters as predictors (table 1; electronic supplementary material, table S1). As several explanatory parameters correlated with each other, single-predictor models were used. Statistical significance of the predictors was assessed using the likelihood ratio test (LRT).

Environmental data were obtained from the hydrometric and meteorological stations located in the Narva River area (Estonian Environment Agency).

3. Results

European eels ($N = 38$), tagged with coded acoustic transmitters, were tracked with stationary receivers in riverine and marine environments during their spawning migration. Eight of the 38 specimens (21%) that migrated to the Baltic Sea from the Narva River reservoir returned to the Narva River (95% CI 10–37%; figure 2; tables 1 and 2; electronic supplementary material, table S1). All eels that returned to the Narva River migrated back to the sea after a period spent in the river. Three of the eight eels were subsequently detected beyond the Baltic Sea in the Danish Straits. The migration of these fish took 68 to 199 days, starting with the second descent to the Baltic Sea in 2019 (July, October and November) and lasting until detection in the Danish Straits (about 1300 km from the river) during the following winter (tables 1 and 2).

Most eels reached the sea for the first time in October and November 2018 (30 individuals; table 1), i.e. soon after release on 24 October. No eels descended during the subsequent winter, and the remaining eight eels reached the sea later, between April and October 2019.

The probability of tagged individuals ascending back to the river from the sea did not depend on fish phenotypic characteristics or environmental factors (LRT; all $p \geq 0.1$; tables 1 and 2; electronic supplementary material, table S1).

Of the 30 fish that did not return to the river, five were subsequently detected in the Danish Straits (table 1). The sizes and maturation indexes of these fish were diverse. One tagged fish was recaptured in the Gulf of Finland (Luga Bay) 50 km northeast of the Narva River outflow in October 2019 (table 1).

Movement patterns of the individuals that returned to the river are described schematically in figure 2 (see also table 2). Fish typically returned to the river 11 to 12 months after first descending to the sea in October and November 2019. Other fish returned earlier. Environmental factors, such as temperature, discharge, moon phase and precipitation, varied widely depending on the time of arrival (table 2). The longest upstream migration was to an impassable barrier located 15 km upstream from the river mouth. The returning eels spent up to 33 days in the river before returning to the sea.

4. Discussion

Our results reveal that silver eels migrating to spawn may show unexpected behaviour after descending to the sea. Instead of starting to move towards the ocean, some fish returned to freshwater after spending a period in the marine environment before subsequently moving to the sea again. This kind of behaviour was exhibited by 21% of the tagged specimens in the study. This is an impressive case in animal ecology, showing how a semelparous species, which invests heavily in building its reproductive potential and faces a particularly challenging

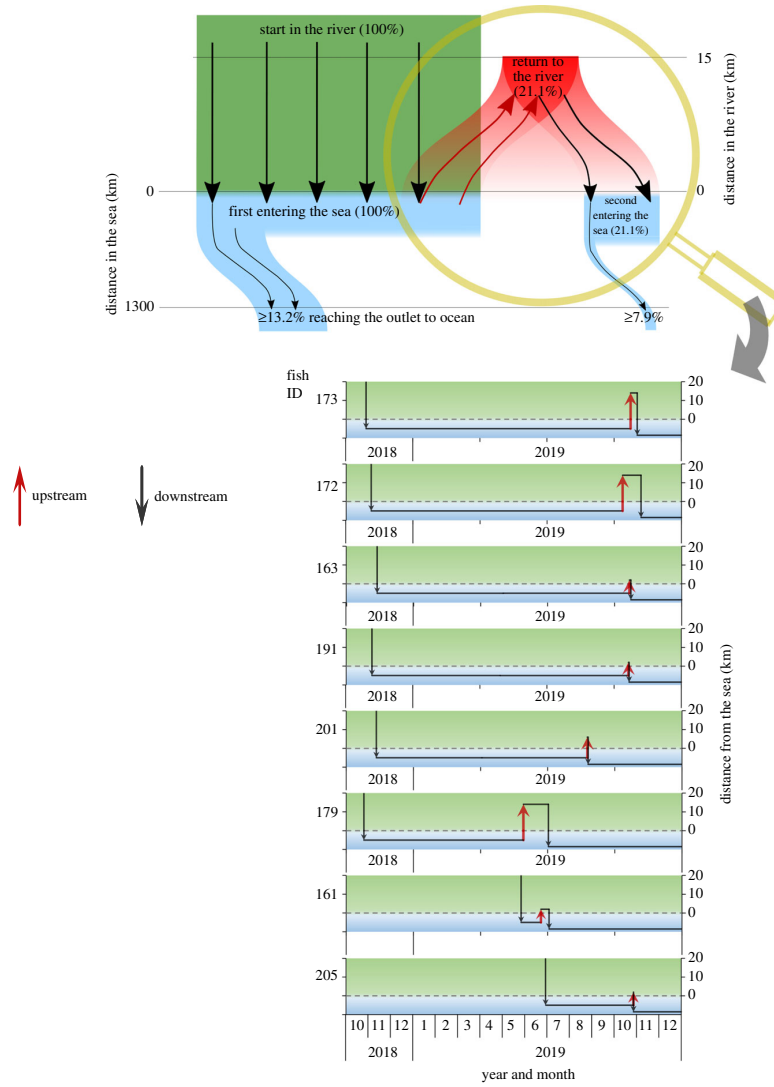

Figure 2. Migration patterns of telemetrically tagged silver European eels. Upper panel: arrows on green background indicate fish ($N = 38$) first descending from the Narva River to the Baltic Sea, arrows on red ascending back to the Narva River with the second migration to the sea, arrows on blue migration in the sea to the Danish Straits (outlet to the ocean). Lower panel: schematic description of the silver European eel individuals moving to the Baltic Sea, back to the Narva River and again to the sea. Movements to the sea are indicated with black arrows, movements to the river with red arrows. The horizontal continuous lines between arrows indicate the duration of freshwater or brackish water phases. The spatial extent of movements in the sea is not known (except for fish with ID nos. 161, 163 and 173 after second descent to the sea).

Table 2. Tracks of the riverine movements of silver European eels after returning to the Narva River from the Baltic Sea and environmental data. The water temperatures and discharges during the fish return to the river are based on daily averages of River Narva. Moon phase during return to the river is expressed as moon illumination rate (at New Moon and Full Moon the per cent illuminated is 0 and 100%, respectively). See the location of each receiver on the map (electronic supplementary material, figure S1).

eel ID	date returning from the sea to the river	length of upstream movement in the river (km)	number of stationary receivers	date reaching to the most upstream location	date leaving the most upstream location	date of second entering the sea	temperature (°C)	discharge ($m^3\ s^{-1}$)	moon phase (%)	participation (mm day^{-1})
161	23.06.2019	1	1	25.06.2019	02.07.2019	04.07.2019	21.6	348	69	0.0
163	21.10.2019	1	1	22.10.2019	22.10.2019	23.10.2019	8.8	407	51	0.3
172	12.10.2019	15	5	21.10.2019	23.10.2019	06.11.2019	8.5	404	98	12.2
173	23.10.2019	14	4	24.10.2019	24.10.2019	01.11.2019	8.7	431	29	0.1
179	30.05.2019	14	4	03.06.2019	03.06.2019	03.07.2019	14.9	438	17	0.0
191	20.10.2019	1	1	21.10.2019	21.10.2019	21.10.2019	8.5	333	62	4.8
201	25.08.2019	5	2	25.08.2019	26.08.2019	26.08.2019	19.1	203	32	0
205	27.10.2019	1	1	27.10.2019	27.10.2019	27.10.2019	8.9	447	1	20

migratory route, could develop sophisticated strategies for regulating its migration. In addition to adjusting the timing of migration, eels can temporarily migrate in the opposite direction of their spawning migration target in the Sargasso Sea. Recognition of this behaviour may be important for better understanding of spawning migration and has a potential impact on the management and conservation of the species.

Movements from the sea into freshwater are common for eels during their growth phase (for yellow eels, [31–34]), but has not been previously documented for the post-feeding stage (silver eels). In our study, factors that could determine the temporary return of silver eels to the river remain obscured. After first descending to the sea, the interruption of eel spawning migration at sea could be linked to the restart of feeding [17,24] or some other factor (e.g. orientation problems, [23]). Nevertheless, the temporary return of silver eels to the river is probably not associated with feeding in the riverine environment, as the feeding activity of eels ceases when the water temperature is less than 10°C [35]. Half the returns occurred at lower water temperatures (8.5–8.9°C). In addition, the standard phenotypic characteristics (size, maturation, etc.) or environmental factors (temperature, discharge, etc.) tested in logistic regression models failed to account for the returning behaviour. Eels in this study were restocked as elvers or glass eels. Therefore, the temporary return can be inherent to eels of some specific ecotype and may be revealed in situations in which fish are removed from their natural habitats and translocated to an area with different environmental conditions (see also [36–38]). Although the reasons why it takes a long time for eels to navigate through the Gulf of Finland and the Baltic Sea on their way to the ocean, and why some fish behaved as 'false starters' remain unresolved, the migration pattern found is an important addition to the description of the plastic behaviour of eels, especially at the beginning of the complex marine phase of their spawning migration (e.g. [12,17,19,20]).

From a management perspective, it is important to note that the fish in this study returned to the river mainly in October and November of the following year, which is known as the main spawning migration season [39,40]. This means these returning eels may join those that are migrating towards the sea for the first time. If the estimation of silver eel escapement relies on direct fishing or counting the migrating specimens and does not consider the possibility of returning specimens, the tally of migrating eels may be incorrect. As a result, escapement may be overestimated, as individuals are counted twice. Rather than counting eels from the same escapement year, specimens from the previous year may be included in the count. In addition, the returning silver eels are once more subject to local fishing and predation (by seals, cormorants or other fish species [41,42]), likely increasing their mortality. Taking such a subgroup of returning silver eels into account and regulating fisheries accordingly can help decrease the mortality and increase the success of migrating silver eels reaching spawning grounds.

We have shown that there may be an undiscovered component in the chain of events guiding eels from the coastal sea to the spawning grounds—a temporary return to the river. We need to be aware that the behaviour of eels can be very diverse in the early stages of spawning migration. Subgroups with different migration strategies can increase the plasticity of the population, which can be particularly important in a changing environment. In order to protect critically endangered European eels, it is necessary to consider the specific needs of the subgroup described in this study and to

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adapt relevant conservation measures. The 'false starts' of silver phase eels may be more common in anguillid eels than thought and continued research on this phenomenon on stocked and naturally invading eels is needed.

Ethics. Fish tagging and release were carried out in accordance with License 1-3/19/1363 (Environmental Board of Estonia).

Data accessibility. Data supporting the current study are provided in the electronic supplementary material [43].

Authors' contributions. All authors participated in fieldwork and article preparation. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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References

1. Aoyama J. 2009 Life history and evolution of migration in Catadromous Eels (Genus Anguilla). *Aqua – BioSci. Monogr.* **2**, 1–42. (doi:10.5047/absm.2009.00201.0001)
2. Bruijs MCM, Durif CMF. 2009. Silver eel migration and behaviour. In *Spawning migration of the European eel*, pp. 65–95. Berlin, Germany: Springer.
3. Righton D, Westerberg H, Feunteun E, Økland F, Gargan P, Amilhat E, Simon J. 2016 Empirical observations of the spawning migration of European eels: the long and dangerous road to the Sargasso Sea. *Sci. Adv.* **2**, e1501694. (doi:10.1126/sciadv.1501694)
4. Durif CMF, Diserud OH, Sandlund OT, Thorstad EB, Poole R, Bergesen K, Vøllestad LA. 2020 Age of European silver eels during a period of declining abundance in Norway. *Ecol. Evol.* **10**, 4801–4815. (doi:10.1002/ece3.6234)
5. Yokouchi K, Daverat F, Miller MJ, Fukuda N, Sudo R, Tsukamoto K, Poole WR. 2018 Growth potential can affect timing of maturity in a long-lived semelparous fish. *Biol. Lett.* **14**, 20180269. (doi:10.1098/rsbl.2018.0269)
6. Amilhat E, Basic T, Beaulaton L, Belpaire C, Bernotas P, Briand C, Wickström H. 2019 Joint EIFAAC/ICES/GFCM working group on eels (WGEEL). *ICES Sci. Rep.* **1**, 1–177. (doi:0.17895/ices.pub.5545)
7. Pike C, Crook V, Gollock M. 2020 Anguilla anguilla. The IUCN Red List of threatened species 2020: e.T60344A152845178.
8. Trancart T, Carpentier A, Acou A, Charrier F, Mazel V, Danet V, Feunteun É. 2020 When 'safe' dams kill: analyzing combination of impacts of overflow dams on the migration of silver eels. *Ecol. Eng.* **145**, 105741. (doi:10.1016/j.ecoleng.2020.105741)
9. Jacobsen MW, Pujolar JM, Pedersen L, Hansen MM. 2018 Single nucleotide polymorphism markers for assessing potential maternal population structure in European eel (Anguilla anguilla). *Conserv. Genet. Res.* **10**, 907–909. (doi:10.1007/s12686-017-0917-8)
10. Tesch FW, Bartsch P, Berg R, Gabriel O, Henderson IW, Kamstra A, Thorpe JE. 2003 *The Eel*. Oxford, UK: Blackwell Science.
11. European Council. 2007 Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. *Official J. Eur. Union* **248**, 17–23.
12. Béguer-Pon M, Dodson JJ, Castonguay M, Jellyman D, Aarestrup K, Tsukamoto K. 2018 Tracking anguillid eels: five decades of telemetry-based research. *Mar. Freshw. Res.* **69**, 199–219. (doi:10.1071/MF17137)
13. Aarestrup K, Thorstad EB, Koed A, Jepsen N, Svendsen JC, Pedersen MI, Økland F. 2008 Survival and behaviour of European silver eel in late freshwater and early marine phase during spring migration. *Fish. Manage. Ecol.* **15**, 435–440. (doi:10.1111/j.1365-2400.2008.00639.x)
14. Bultel E, Lasne E, Acou A, Guillaudeau J, Bertier C, Feunteun E. 2014 Migration behaviour of silver eels (Anguilla anguilla) in a large estuary of Western Europe inferred from acoustic telemetry. *Estuarine Coastal Shelf Sci.* **137**, 23–31. (doi:10.1016/j.ecss.2013.11.023)
15. Frankowski J, Dorow M, Juenger J, Reckordt M, Schulz S, Ubl C, Winkler H. 2019 Behaviour, escapement and mortality of female European silver eels within a regulated lowland river draining into the Baltic Sea. *Fish. Manage. Ecol.* **26**, 86–96. (doi:10.1111/fme.12307)
16. Travade F, Larinier M, Subra S, Gomes P, De-Oliveira E. 2010 Behaviour and passage of European silver eels (Anguilla anguilla) at a small hydropower plant during their downstream migration. *Knowledge Manage. Aquatic Ecosyst.* **398**, 1. (doi:10.1051/kmae/2010022)
17. Barry J, Newton M, Dodd JA, Lucas MC, Boylan P, Adams CE. 2016 Freshwater and coastal migration patterns in the silver-stage eel Anguilla anguilla. *J. Fish Biol.* **88**, 676–689. (doi:10.1111/jfb.12865)
18. Durif CMF, Dufour S, Elie P. 2005 The silvering process of Anguilla anguilla : a new classification from the yellow resident to the silver migrating stage. *J. Fish Biol.* **66**, 1025–1043. (doi:10.1111/j.1095-8649.2005.00662.x)
19. Sjöberg NB, Wickström H, Asp A, Petersson E. 2016 Migration of eels tagged in the Baltic Sea and Lake Mälaren-in the context of the stocking question. *Ecol. Freshw. Fish (May)* **26**, 517–532. (doi:10.1111/eff.12296)
20. Stein F, Doering-Arjes P, Fladung E, Brämick U, Bendall B, Schröder B. 2016 Downstream migration of the European eel (Anguilla anguilla) in the Elbe River, Germany: movement patterns and the potential impact of environmental factors. *River Res. Appl.* **32**, 666–676. (doi:10.1002/rra.2881)
21. Crook DA, Macdonald JI, Morrongiello JR, Belcher CA, Lovett D, Walker A, Nicol SJ. 2014 Environmental cues and extended estuarine residence in seaward migrating eels (*Anguilla australis*). *Freshw. Biol.* **59**, 1710–1720. (doi:10.1111/fwb.12376)
22. Vøllestad LA, Jonsson B, Hvidsten NA, Næesje TF. 1994 Experimental test of environmental factors influencing the seaward migration of European silver eels. *J. Fish Biol.* **45**, 641–651. (doi:10.1111/j.1095-8649.1994.tb00930.x)
23. Westin L. 1998 The spawning migration of European silver eel (Anguilla anguilla L.) with particular reference to stocked eel in the Baltic. *Fish. Res.* **38**, 257–270. (doi:10.1016/S0165-7836(98)00162-3)
24. Svedäng H, Wickstrom H. 1997 Low fat contents in female silver eels: indications of insufficient energetic stores for migration and gonadal development. *J. Fish Biol.* **50**, 475–486. (doi:10.1006/jfbi.1996.0313)
25. Verhelst P, Bruneel S, Reubens J, Coeck J, Goethals P, Oldoni D, Mouton A. 2018 Selective tidal stream transport in silver European eel (Anguilla anguilla L.)—Migration behaviour in a dynamic estuary. *Estuarine Coastal Shelf Sci.* **213**, 260–268. (doi:10.1016/j.ecss.2018.08.025)
26. Järvalt A, Kask M, Krause T, Palm A, Tambets M. 2010 *Potential downstream escapement of European Eel from L. Peipsi Basin (Estonia-Russia)*, pp. 1–11. Ohrid, Republic of Macedonia: Balwois.Com.
27. Kniebusch M, Meier HEM, Radtke H. 2019 Changing salinity gradients in the Baltic Sea as a consequence of altered freshwater budgets. *Geophys. Res. Lett.* **46**, 9739–9747. (doi:10.1029/2019GL083902)
28. Winsor P, Rodhe J, Omstedt A. 2003 Erratum: Baltic Sea ocean climate: an analysis of 100 yr of hydrographical data with focus on the freshwater budget. 18:5-15, 2001. *Clim. Res.* **25**, 183. (doi:10.3354/cr018005)
29. Durif C, Guibert A, Pierre E. 2009 Morphological discrimination of the silvering stages of the European eel. Eels at the Edge. Science, Status, and Conservation Concerns. *Am. Fish. Soc. Symp.* **58**, 103–111. (doi:10.1111/j.1095-8649.2010.02758.x)
30. Team RC. 2020 *R: a language and environment for statistical computing; version 4.0. 2*. Vienna, Austria: R Foundation for Statistical Computing.
31. Arai T, Kotake A, McCarthy TK. 2006 Habitat use by the European eel Anguilla anguilla in Irish waters. *Estuarine Coastal Shelf Sci.* **67**, 569–578. (doi:10.1016/j.ecss.2006.01.001)
32. Daverat F, Limburg KE, Thibault I, Shiao J-C, Dodson JJ, Caron F, Tzeng W-N, Iizuka Y, Wickström H. 2006

Phenotypic plasticity of habitat use by three temperate eel species, Anguilla anguilla, A. japonica and A. rostrata. *Mar. Ecol. Prog. Ser.* **308**, 231–241. (doi:10.3354/meps308231)

33. Sweezey M. 2014 Seasonal migrations of the American eel, Anguilla rostrata, in the Upper Salmon River, New Brunswick, Doctoral dissertation. University of New Brunswick.
34. Tzeng WN, Wang CH, Wickström H, Reizenstein M. 2000 Occurrence of the semi-catadromous European eel Anguilla anguilla in the Baltic Sea. *Mar. Biol.* **137**, 93–98. (doi:10.1007/s002270000330)
35. Sadler K. 1979 Effects of temperature on the growth and survival of the European eel, Anguilla anguilla L. *J. Fish Biol.* **15**, 499–507. (doi:10.1111/j.1095-8649.1979.tb03633.x)
36. Drouineau H, Durif C, Castonguay M, Mateo M, Rochard E, Verreault G, Youkouchi K, Lambert P. 2018 Endangered eels: a symbol of the effects of global change. *Fish Fish.* **19**, 903–930. (doi:10.1111/faf.12300)
37. Mateo M, Lambert P, Tétard S, Castonguay M, Ernande B, Drouineau H. 2017 Cause or consequence? Exploring the role of phenotypic plasticity and genetic polymorphism in the emergence of phenotypic spatial patterns of the European eel. *Can. J. Fish. Aquat. Sci.* **74**, 987–999. (doi:10.1139/cjfas-2016-0214)
38. Pavey SA, Gaudin J, Normandeau E, Dionne M, Castonguay M, Audet C, Bernatchez L. 2015 RAD-sequencing highlights polygenic discrimination of habitat ecotypes in the panmictic American eel (Anguilla rostrata). *Curr. Biol.* **25**, 1666–1671. (doi:10.1016/j.cub.2015.04.062)
39. Sandlund OT, Diserud OH, Poole R, Bergesen K, Dillane M, Rogan G, Vøllestad LA. 2017 Timing and pattern of annual silver eel migration in two European watersheds are determined by similar cues. *Ecol. Evol.* **7**, 5956–5966. (doi:doi.org/10.1002/ece3.3099)
40. Teichert N, Tétard S, Trancart T, de Oliveira E, Acou A, Carpentier A, Feunteun E. 2020 Towards transferability in fish migration models: a generic operational tool for predicting silver eel migration in rivers. *Sci. Total Environ.* **739**, 140069. (doi:10.1016/j.scitotenv.2020.140069)
41. Hansson S, Bergström U, Bonsdorff E, Härkönen T, Jepsen N, Kautsky L, Vetemaa M. 2018 Competition for the fish - Fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. *ICES J. Mar. Sci.* **75**, 999–1008. (doi:10.1093/icesjms/fsx207)
42. Tverin M, Esparza-Salas R, Strömberg A, Tang P, Kokkonen I, Herrero A, Lundström K. 2019 Complementary methods assessing short and long-term prey of a marine top predator – Application to the grey seal-fishery conflict in the Baltic Sea. *PLoS ONE* **14**, 1–26. (doi:10.1371/journal.pone.0208694)
43. Tambets M, Kärgenberg E, Järvalt A, Økland F, Kristensen ML, Koed A, Bernotas P. 2021 Migrating silver eels return from the sea to the river of origin after a false start. (doi:10.6084/m9.figshare.c.5574214)

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