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JUSTAS DAINYS

MIGRATION OF STOCKED EUROPEAN EELS (*ANGUILLA ANGUILLA* L.) IN LITHUANIA AND POTENTIAL CONTRIBUTION TO SPAWNING STOCK RESTORATION

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VILNIAUS UNIVERSITETAS
GAMTOS TYRIMŲ CENTRAS

JUSTAS DAINYS

ĮŽUVINTŲ EUROPINIŲ UNGURIŲ (*ANGUILLA ANGUILLA* L.) MIGRACIJA LIETUVOJE IR POTENCIALUS INDĖLIS Į NERŠTINIŲ IŠTEKLIŲ ATKŪRIMĄ

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Contents

Papers:

ABBREVIATIONS

EMP – Eel Management Plan

EU – European Union

FCF – Fulton’s Condition Factor

HPP – Hydro-power Plant

ICES – The International Council for the Exploration of the Sea

MS – Migration success

INTRODUCTION

Relevance of the study. According to the Food and Agriculture Organization of the United Nations, over 70% of fish populations are fully used, overused or depleted. The European eel (*Anguilla anguilla*) in particular is one of the most severely affected species. Steep decline in European eel recruitment started in the 1980s and since then eel population abundance has fallen below safe biological limits, with estimates of decline in rates of recruitment ranging from 50% to 99% (ICES, 2010; Jacoby and Gollock, 2014). This population depletion has occurred over the entire range of this species' distribution without a single obvious cause. In response to declines in eel stocks, in 2007 the European Union issued the Regulation of European Council No. 1100/2007, which lays down measures for stock restoration of European eels. The regulation obliges member states to develop national Eel Management Plans. A Lithuanian national eel management plan was approved by European Commission in 2009. The aim of these plans is to restore stocks to sustainable levels, akin to their historical abundance. Restocking of inland waters is considered one of the main tools to accomplish this aim (Dekker and Beaulaton, 2016), but stocking with hatchery-reared fish does not always deliver significant improvements in fish stocks (Larscheid, 1995; Blaxter, 2000). There have been suggestions that eels derived from stocking are less likely to contribute to the spawning stock than those that are produced naturally.

Nowadays, after capture in the wild, glass eels are often on-grown in aquaculture before restocking them into natural water bodies. It has been commonly believed that mortality upon release of these on-grown eels back into the wild is lower when compared with mortality rates among those stocked at the glass eel stage. This tenet is speculative and in need of testing (ICES, 2015b). After several years or even decades spent in fresh or brackish waters, eels previously released from aquaculture farms reach the silver eel stage and start their downstream spawning migration. Results of previous studies (Winter et al., 2006; Winter et al., 2007; Bruijs and Durif, 2009; Aarestrup et al., 2010) have demonstrated that substantial mortality during this migration dramatically reduces the number of spawners. Fishing mortality and injury during passage through HPPs are often considered to be the main causes of eel mortality in rivers (Winter et al., 2006).

There is a general assumption is that turbine related mortality of migrating fish decreases with increasing turbine size (Calles et al., 2010), but eel mortality rates in HPPs are highly variable depending on river physiography, associated hydrological conditions and the type of migration barriers installed (ICES, 2007). Kaplan turbines which are the most commonly used in Europe have been the intensively studied type of HPP and eel morality during passage through these turbines has been reported as ranging between 15% and 30% in large models, and from 50% to 100% in the smaller turbines used in most small-scale HPPs (Monten, 1985; Hadderingh and Baker, 1998). Unlike Kaplan turbines, rates of eel mortality in cross-flow turbines (e.g. Banki, CINK, Ossberger) that are also used in some small-scale HPPs have never been previously studied. These turbines are likely to have a severe impact on migrating eels because mortality rates among other fish species whose passage through cross-flow turbines has been studied have been shown to be significantly higher (up to 75%; Gloss and Wahl, 1983; DuBois and Gloss, 1993) compared to that in Kaplan or Francis turbines. Nevertheless, according to Ložys et al. (2008), approximately half of the Lithuanian eel population is not affected by HPP turbines during downstream migrations. Although there have been numerous studies about eel mortality arising from passage through various HPPs, there are scant data available on eel escapement success or downstream migration speed within unimpeded rivers (e.g. Simon et al., 2011; Bultel et al., 2014; Stein et al., 2016) and lagoons (e.g. Amilhat et al., 2008, Charrier et al., 2012). Moreover, Lithuania’s lowland rivers differ in terms of their hydrological conditions (40% of discharge comes from melted snow, 35%

from ground water and only 25% from rain); temperature (2–3 months per year rivers are covered with ice); degree of regulation (most large rivers are natural and historically were not regulated); and flow regime (in spring due to melting snow discharge, flows are 2–3 times higher than in other seasons) compared to Western Europe (Gailiušis et al., 2001). In the context of concerted international efforts to restore eel stocks, it is therefore essential for successful implementation of the national Eel Management Plans to determine the main downstream migration patterns and escapement success of silver eels in the North-Eastern region of their distribution range.

Downstream migration of eels in Lithuania ends when silver eels enter the Curonian Lagoon and from there finally reach the Baltic Sea via the Klaipeda Strait. During the final silvering stage eels do not feed during their oceanic migration phase (Tesch, 2003; Van den Thillart and Dufour, 2009), therefore they must rely completely on accumulating sufficient fat stores during the sedentary yellow eel stage which is spent in coastal or inland waters to obtain energy for migration and gonad maturation (Tesch, 2003). The migration distance to the presumed spawning areas in the Sargasso Sea is at least 4000 km, but from different regions within the species' range may differ up to more than 3500 km (Schmidt, 1923; Clevestam et al., 2011). Eels migrating from the North-Eastern region of their distribution range obviously need more energetic resources and more time to reach the the Sargasso Sea, compared to eels migrating from the Atlantic coast bordering Western Europe. Eels migrating from the inland waters of Eastern Lithuania must cover almost 8000 km (Paper IV). All eels inhabiting inland Lithuanian waters are known to be of stocked origin (Shiao et al., 2006; Lin et al., 2007; Ložys et al., 2008; Ragauskas et al., 2014). Moreover, prior to stocking, glass eels must be translocated by freight for more than 2000 kilometres from the United Kingdom or France and then released into Lithuanian inland waters. Due to a lack of data about energy resources among stocked eels migrating to spawn, it is unclear if European eels translocated over long distances prior to stocking have sufficient capacity to accommodate the extended distances of migration caused by human intervention. Inability of stocked eels in North America to accumulate adequate fat reserves for migration and reproduction has been reported by Couillard et al. (2014). An evaluation of the migratory potential of Lithuanian silver eels of stocked origin to reach their natural spawning grounds is important in gaining a better understanding of the contribution of stocking activities towards recovery of European eel stocks.

Scientific novelty of the study:

1. A unique laboratory experiment undertaken within this study indicated that after transitioning to natural food (*Chironomus spp.* larvae) on-grown eels had no advantage in survival compared with glass eels.
2. It was estimated that eels passing through small CINK turbines suffer lethal injuries resulting in 100% mortality.
3. It was demonstrated that a substantial proportion of eels migrating downstream used fish ladders, originally designed for upstream migration of salmonids.
4. Speed of migration and migration success of silver eels were determined in lowland rivers of the North-Eastern part of the species distribution range.
5. Swimming potential for silver eels of stocked origin was estimated for the North-Eastern part of the species distribution range.

Scientific and practical significance. Results of the present study allow optimization of measures towards the recovery of European eel stocks. Stocking of eels is one of the main actions carried out to restore stocks to sustainable levels in most European countries. Ongrowing eels prior to stocking has been a widely accepted practice due to the perception that mortality upon release of on-grown eels back into the wild is lower compared to mortality rates among those which have been stocked at glass eel stage. In contrast with this notion, results of the laboratory study on eel survival under treatment with natural food, indicated that survival decreases with increasing duration of the on-growing period and on-grown eels have no advantage in survival compared to glass eels when fed natural food (*Chironomus* spp. larvae). This finding is an essential contribution towards a better understanding of how well eels on-grown in aquaculture can wean from artificial to natural food and how this transition affects their survival in comparison with wild glass eels. Practical application of this finding is important when considering the efficacy of measures targeting restoration of depleted eel stocks to sustainable levels. This is especially the case when restocking of inland waters is one of the main measures for accomplishing restoration. It is for this reason that results of the current study are of interest to a broad readership working in the fields of fisheries, aquaculture and ecological restoration.

After stocked eels mature and reach silver eel stage, they start migrating downstream towards the sea or ocean. During these migrations substantial mortality can drastically reduce the number of successful spawners. Success of Eel Management Plans and restoration activities is gauged in the context EU Regulations by determining in the numbers of silver eels leaving inland waters to spawn. Barriers, especially hydropower installations, are considered to be one of the major threats for eels' downstream spawning migration. Therefore, it is important to determine the extent to which downstream migrating eels use fish ladders originally designed for upstream migration of salmonids and to estimate the proportion of migrating eels which are killed by passing directly through turbines. This study provides an estimate of the mortality rate among downstream migrating eels passing through (1) a hydropower plant with Kaplan turbines and a fish ladder, and (2) a cross-flow CINK turbine. The latter has never been reported before, hence the study provides critical information for both fundamental and applied science. Additionally, the proportion of downstream migrating eels passing through the fish ladder was estimated. Results of the study demonstrated that HPPs may significantly threaten the escapement targets set in eel management plans if stocking is carried out in water bodies upstream from HPPs. This aspect of eel mortality must be taken into account whenever long term strategies for restoration of depleted eel populations are considered. Determination of the patterns of silver eel migration in the rivers of the North Eastern eel distribution range is important in the context of concerted international efforts to restore eel stocks and also provided valuable new data for further research.

Eels have the longest spawning migration route amongst all known fish species and critically they do not feed during their oceanic migrations. Spawning from eels of stocked origin has previously been reported as being insufficient for restoring recruitment. This is based on a presumption that they possess lower energetic resources than eels which have spent their entire lives in the wild (Couillard et al., 2014). Despite suggestions that eels derived from stocking are less likely to contribute to the spawning stock due to lower fitness related to insufficiency of energetic resources, results of the current study provide important evidence to the contrary. The results showed that more than one third of glass eels sourced from up to 2000 km away and subsequently released into inland waters of Lithuania, representing the North-Eastern part of their distribution range, had sufficient energetic resources to successfully reproduce. It can be surmised that stocked eels are likely to contribute to the spawning stock if their navigational abilities in migrating to the ocean are adequate.

The key aim of the study was to evaluate the potential of eels stocked into inland water bodies within the North-Eastern region of their geographical distribution range to contribute to the global spawning stock.

Study objectives:

1. To evaluate how well on-grown eels wean from artificial to natural food (*Chironomus* spp. larvae) and how this transition affects their survival in comparison with wild glass eels.
2. To evaluate eel mortality caused by different types of hydropower turbines: large Kaplan turbine, small Kaplan turbine and small CINK turbine.
3. To evaluate the success and speed of eels migrating downstream to the Curonian Lagoon and Baltic Sea.
4. To assess whether or not eels translocated from the coasts of Western Europe to the North-Eastern extremity of their distribution range accumulate enough energy for gonadal maturation and migration to their spawning grounds in the Sargasso Sea.

Statements to be defended:

1. Eels ongrown in an aquaculture facility have no advantage in survival compared to glass eels after transition to natural food (*Chironomus* spp. larvae).
2. Turbine induced mortality is highly dependent on turbine size and type; Kaplan turbines are more eel-friendly compared to cross-flow CINK turbines. Turbine-related mortality can dramatically reduce the number of spawners returning to the spawning grounds, threatening escapement targets of management measures if stocking occcurs upstream from hydropower plants.
3. Average eel migration speed in rivers and in the Curonian Lagoon are similar, but escapement success from the Lagoon into the Baltic Sea was significantly higher than escapement from the river system into the Lagoon.

4. Despite the major spawning migration of eels commencing during early spring within inland Lithuanian waterbodies, the peak of eel emigration to the Baltic Sea occurs in mid or late autumn.
5. More than one third of silver eels that were previously translocated for a considerable distance and then released into inland waters of the North-Eastern region of their distribution range had sufficient energetic resources for successful spawning migration and gonadal maturation.

Scientific approval and publications. The results of the present study are summarized in four scientific publications (Papers I-IV) and were presented at eight national and international scientific conferences.

Structure of the thesis. The thesis consists of the following chapters: Abbreviations, Introduction, Literature review, Materials and Methods, Results and Discussion, Conclusion, Recommendations, Reference List, Articles on the subject of the thesis.

List of papers. The thesis is based on the following papers referred to in the text by Roman numeral.

I. J. Dainys, H. Gorfine, E. Šidagytė, E. Jakubavičiūtė, M. Kirka, Ž. Pūtys, L. Ložys. 2017. Do young on-grown eels, *Anguilla anguilla* (Linnaeus, 1758), outperform glass eels after transition to a natural prey diet? Journal of Applied Ichthyology, 33:361–365. DOI: 10.1111/jai.13347

II. J. Dainys, S. Stakėnas, H. Gorfine, L. Ložys. Mortality of Silver Eels, *Anguilla anguilla* (Linnaeus, 1758), Migrating Through Different Types of Hydropower Turbines in Lithuania. (Submitted).

III. J. Dainys, S. Stakėnas, H. Gorfine, L. Ložys. 2017. Silver eel, *Anguilla anguilla* (Linnaeus, 1758), migration patterns in lowland rivers and lagoons in the North-Eastern region of their distribution range. (Accepted, Journal of Applied Ichthyology). DOI: 10.1111/jai.13426

IV. J. Dainys, H. Gorfine, E. Šidagytė, E. Jakubavičiūtė, M. Kirka, Ž. Pūtys, L. Ložys. Are Lithuanian Eels, *Anguilla anguilla* (Linnaeus, 1758), Fat Enough To Reach the Spawning Grounds? (Submitted).

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1. LITERATURE REVIEW

In this section a short literature review on biology and main aspects of European eel (*Anguilla anguilla*) ecology is presented. More detailed reviews of scientific literature dealing respectively with relevant biological/ecological issues are presented in each paper.

1.1 General life history. The European eel, *Anguilla anguilla* (L.), is one among 15 to 18 species of the genus *Anguilla* (Family *Anguillidae*, „Freshwater eels“) (Wickström, 2001), but taxonomic composition of this family is not yet stable (Eschmeyer, 2014). The species is facultatively catadromous, living in fresh, brackish and coastal waters but migrating to pelagic marine waters to breed (Jacoby and Gollock, 2014). Its geographic distribution extends from the North Cape in Northern Norway, southwards along the coast of Europe, along the entire Mediterranean coastline, and on the North African Coast (Jacoby and Gollock, 2014). Presumptive spawning grounds are located in the Sargasso Sea, situated between the Bermuda Islands and Puerto Rico where circumstantial evidence points towards both Atlantic eel species (*A. anguilla* and *A. rostrata*) spawning (Schmidt, 1925; Tesch, 1977). This presumption is made because the smallest sized eel larvae called *leptocephali* are found in this area (Schmidt, 1923) with a spatial trend of increasing size towards the coasts of the Europe. There is no direct evidence as silver eels have never been observed spawning in the ocean (Tsukamoto, 2009). The earliest larval stages caught in the Sargasso Sea contain the remnants of an oil droplet which is part of the yolk sack of the egg. When eel larvae start feeding they transform into a transparent leaf-shaped morphotype, referred to as *leptocephali*. Oceanic migration of *leptocephali* is estimated to take about two years on average before they arrive at the continental shelf (Tesch, 1977; Bonhommeau et al., 2009). By the time the *leptocephali* reach the continental slope they are as large as c. 100 mm in length and metamorphose into c. 75 mm 0.3 g glass eels which are elongated and have a transparent body (Edeline, 2007). Glass eels enter freshwater as sexually undifferentiated individuals and sex determination is principally driven by environmental factors with density dependency producing more males at high densities (Davey and Jellyman, 2005; Belpaire et al., 2009). These glass eels are observed in the summer and autumn along the Portuguese coasts, and in winter and spring in the North Sea (Jacoby and Gollock, 2014). The start of the glass eel fishing season is dependant on weather conditions but typically lasts from January to March in the United Kingdom and from November to April in France. When the water temperature increases during spring, these glass eels become pigmented and some of them start to ascend fresh water streams and rivers (Wickström, 2001). At this stage they are referred to as elvers. After elvers finish active migration, a sedentary yellow eel stage commences which is the main feeding and growing phase of their lives. The life strategies of males and females differ. From the data available, lower bound age estimates for attaining average length during the continental growth phase are approximately 3–8 years for males and 4–5 years for females with upper bound estimates approximately 12–15 years for males and 18-20 for females (Froese and Pauly, 2005; Durif et al., 2009). Nevertheless, eels are known to be an extremely long-lived fish species with many year classes (up to 50) (Dekker, 2015) and some silver eels caught in the Curonian Lagoon were determined to be as old as 32 years (Ložys and Dainys, 2015). After several years, or even decades, spent in fresh or brackish water, yellow eels mature to reach the silver eel stage and commence their spawning migration which is time-dependent and generally takes places during autumn (Tesch, 1977; Moriarty, 1978; Capoccioni et al., 2014) or even spring (Czeczuga and Czeczuga-Semeniuk, 2000; Ložys et al., 2008).

The spawning migration of the European eel to the Sargasso Sea is one of the greatest migrations in the animal kingdom (Righton et al., 2016). Eels migrating from Lithuanian inland waters must cover more than 7900 km (Paper IV). Migrating silver eels at the final silvering stage do not feed during their migration to the spawning grounds (Van den Thillart and Dufour, 2009).

Instead they rely completely on accumulating sufficient fat stores during the sedentary yellow eel stage, spent in coastal or inland waters, to obtain the energy required for migration and gonad maturation (Tesch, 2003). Survey catches of *leptocephali* larvae suggest that spawning peaks from the beginning of March and continues until July (McCleave, 1993). The adults are assumed to die after spawning (Jacoby and Gollock, 2014).

1.2 Eel stock. According to results from archaeological research, the population of eels in the Baltic region was intensively exploited 5500 years BC (Schmolcke et al., 2006). Steep declines in eel recruitment throughout Europe were not observed until the 1980s (in the Baltic region even earlier) and since then eel population abundance has fallen outside safe biological limits over the entire geographic range (Dekker, 2004; ICES, 2006). Changes in the Gulf stream, migration barriers, fishing pressure, habitat loss, parasites and pollution are the main factors associated with these changes (Feunteun, 2002; Wirth and Bernatchez, 2003; Dekker, 2004), but there is no clear consensus on their relative importance. The impact of anthropogenic and environmental pressures on eels is highly dependent on local conditions and large differences in eel quality and mortality occur among different areas (Kirkegaard, 2010). Information about mortality is either absent (egg and larvae stages) or very limited during different life stages and it is extremely difficult to quantify the extent to which anthropogenic and environmental pressures affect eels.

Contemporary eel populations have been assessed to be outside safe biological limits (Astrom and Dekker, 2007). According to ICES (2009) the abundance of eels for all stages including glass, yellow and silver phases, as well as stock recruitment levels, were at historical minima during 2009. Based on ICES recommendations in 2007 the European Council adopted a framework regulation for the recovery of the European eel stock (Council Regulation (EC) No 1100/2007 of 18. September 2007). Each EU Member State was required to establish a national eel management plan. The main objective of each plan shall be to take actions to reach a rate of escapement to the sea of at least 40% of the total silver eel biomass, relative to the best estimate of escapement that would have existed under pristine conditions (with no anthropogenic pressure). Reducing of anthropogenic mortalities and restocking water bodies with eels is considered to be one of the main actions for the achievement of these aims.

The first known eel transfer and stocking was recorded in France during 1840 (Dekker and Beaulaton, 2016). In the 1920s and 1940s stocking was carried out in many European countries. During this inter-war period eels were stocked predominantly in the United Kingdom, the Netherlands, Germany and Poland, but also in Latvia, Lithuania and Sweden (Dekker and Beaulaton, 2016). Since 1950–1990s numbers of restocked eels have increased significantly: 3682 million (1200 tonnes) glass eels were stocked in Europe from 1945 to 2000. During the stocking peak in 1970s approximately 150 million eels were transferred and restocked annually. As a result, in many countries, restocked eels constituted a substantial proportion of commercial catches.

Stocking of Lithuanian waters with glass eels started in the Vilnius region during 1928 and lasted until 1939. During that period approximately 3.2 million glass eels were released (Mačionis, 1969). Subsequent stocking was carried out in the post-war period during 1956–2007. According to official data a total of 148 lakes and ponds were stocked with 50 million glass and on-grown eels (on average 1.25 million per year) (Ložys et al., 2008). The most intensive stocking period was during 1960–1986 (in total 33.2 million eels were released), while later stocking activities became irregular and only in low numbers. The last considerable stocking, prior to implementation of the Lithuanian Eel Management Plan, was undertaken in 2004 when 70.1 thousand eels were released into Lithuanian water bodies (Fig 1).

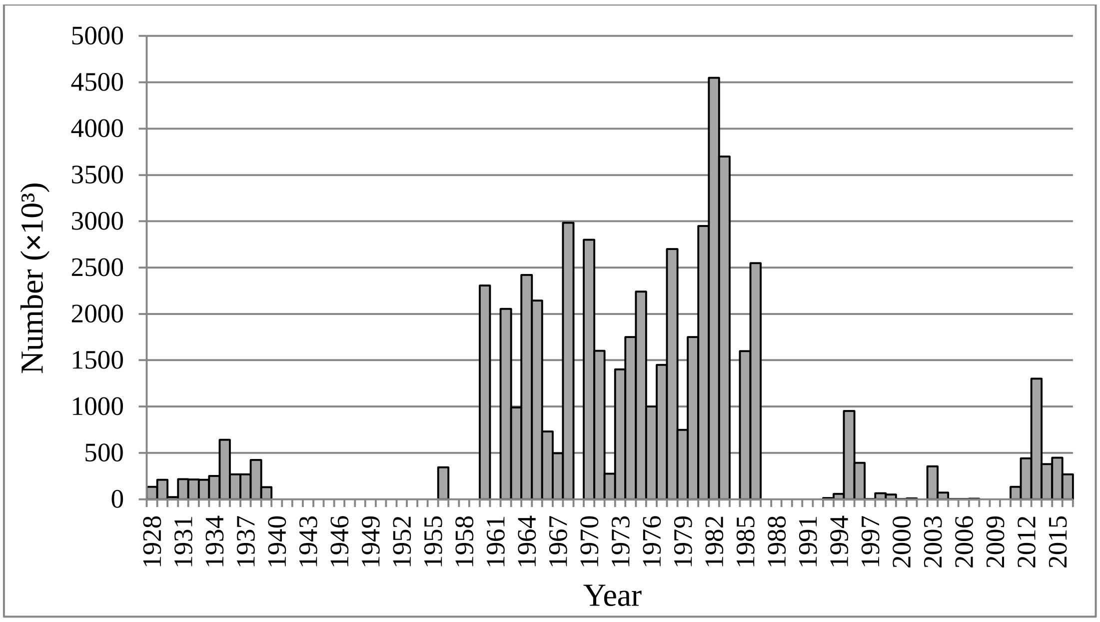

Fig 1. Numbers of eels stocked into Lithuanian water bodies during 1928–2016.

The Lithuanian National Eel Management Plan was approved by the European Commission in 2009 and stocking of waters with glass or ongrown eels was considered to be the main measure to achieve the Plan's objectives. Since then, more intensive eel stocking commenced and almost 3 million ongrown eels were released into 154 different water bodies during 2011–2016.

1.3 Issues related to stocking. Despite the long-term practice of stocking different water bodies throughout Europe, many questions related to the 'best practice' for this activity still remain. ICES (2011) suggests that stocking with glass eel in Europe reached a plateau between 1960 and 1988, and then decreased rapidly. In contrast, since the late 1980s an increase has occurred in the number of small yellow eels used for stocking. It is a common practice to ongrow glass eels in an aquaculture facility for approximately one to three months, especially in Northern Europe due to low temperatures and frozen lakes during the high season of the glass eel fishery in the southern part of the European Atlantic coast. The other reason why glass eels are ongrown in aquaculture facilities prior to release is that their weight increases up to 10-fold during ongrowing period. It is commonly believed that mortality of these eels is lower when compared with mortality rates among glass eels. This tenet, however, is speculative and has not been substantiated with experimental evidence (ICES, 2007; ICES, 2015b).

Moreover, some previous field experiments suggested that stocking with on-grown eels may result in poorer survival rates than for glass eels (Berg and Jørgensen, 1994; Pedersen, 2000; Wickström, 2001; ICES, 2007). Such poorer survival of farmed eels might be related to failure to recognise or respond appropriately to predators (Stunz and Minello, 2001; Alvarez and Nicieza, 2003; Malavasi et al., 2004). Exposure of different fish species to an artificial environment during on-growing has been reported to produce phenotypic changes that give rise to impaired migratory and anti-predator behaviour thereby reducing chances of survival (Brown and Laland, 2001; Svåsand, 2004), and in some instances stocked fish may be unable to adapt to natural food consumed by wild fish (Smirnov et al., 1994). In addition to these negative aspects of rearing eels in a farm, on-growing of glass eels in aquaculture poses risks of spreading parasites and diseases; genotypic population alteration, increase in the proportion of males; release of slower growing individuals caused by size-dependant sorting; and increasing the cost per stocked eel (Egusa, 1979; ICES, 2011). Despite some recent field studies (Simon and Dörner, 2014; Pedersen and Rasmussen, 2016) which do not support the construct that ongrown eels outperform glass eels after release into the wild, there have been no laboratory experiments performed until now to support or reject this hypothesis.

A more detailed literature review of ongrowing effect on eel survival is presented in the paper entitled “Do young on-grown eels, *Anguilla anguilla* (Linnaeus, 1758), outperform glass eels after transition to a natural prey diet?” (Paper I).

After release into the wild, stocked eels spend approximately 6 to 20 years (or even up to 50 (Dekker, 2015)) in the yellow eel stage (Bauchot, 1986). During this sedentary stage eels feed and grow in size, but no intensive maturation processes takes place. At the end of the yellow eel phase, eels undergo a second metamorphosis called ‘silvering’. This metamorphosis corresponds to physiological and morphological changes that prepare the fish for the oceanic migration back to the Sargasso Sea and reproduction there (Durif et al., 2005). During this process, the body becomes silver, the eyes, nostrils and fins enlarge, the gonads develop and atrophy of the alimentary tract takes place. These changes correlate with an increase in gonadosomatic index (Franzellitti et al., 2015). Silver eels of the last silvering stage do not feed during spawning migrations (Van den Thillart and Dufour, 2009). Silver European eels need to cover a minimum of 4000 km to reach the Sargasso Sea (McCleave, 1993) and must expend considerable energy to cover this large distance (Van Ginneken et al., 2005). This suggests that energy reserves, in the form of lipids, may be critical for gonadal maturation and successful migration to the spawning grounds. The inland Lithuanian eel population is comprised solely of eels from stocked origin (Shiao et al., 2006). Prior to stocking, these eels are shipped to Lithuania by plane for more than 2000 kilometres. There have been suggestions that eels derived from aquaculture farms are less likely to contribute to the spawning stock. Couillard et al. (2014) demonstrated that none of the American silver eels (*Anguilla rostrata*) of farmed origin that were migrating downstream had enough energetic reserves to complete migration and maturation, whereas more than half of the silver eels of natural origin had adequate reserves. Consequently, the rationale of re-stocking with farmed eels as an approach to mitigating decline in wild eel populations is increasingly being questioned (Brämick et al., 2016). Overall, there is considerable evidence that stocked eels do survive and escape as silver eels, however, evidence about whether or not they contribute to spawning stock is insufficient. Despite previous studies on fat reserves stored by eels (Tesch, 1977; Boetius and Boetius, 1985; Bergersen and Klemetsen, 1988; Larsson et al., 1990;

Svedäng and Wickström, 1997; Belpaire et al., 2009), it is not yet clear whether eels migrating from the North-Eastern part of their distribution range, especially those of stocked origin which are translocated over long distances, accumulate sufficient energy reserves for successful spawning migration and gonadal maturation. This important issue has been studied in detail during the current study. A detailed literature review s is presented in the paper "Are Lithuanian Eels Fat Enough To Reach The Spawning Grounds?" (Paper IV).

1.4 Anthropogenic mortality. Human impact during the downstream descent of silver eels involves extra mortality attributable to fisheries and hydropower (Feunteun, 2002). The non-fishing anthropogenic mortality factors can be grouped as those due to (a) hydropower; (b) habitat loss or degradation; and (c) pollution, diseases, and parasites (ICES, 2015b). The effect of each factor varies between river systems, depending on the intensity of fisheries, and the number and allocation of hydropower plants within a catchment area. Fisheries impact on all available continental life stages throughout the distribution area, although fishing pressure varies from area to area, from almost nil to heavy overexploitation (ICES, 2015a). Total landings and effort data are incomplete and therefore ICES does not have the information needed to provide a reliable estimate of total catches of eel (ICES, 2015a). Nevertheless, in the years since the implementation of the EU eel regulation, fishing restrictions in many countries appear to have reduced the catches considerably (ICES, 2016). In Lithuania some measures to reduce fishing mortality are also taken in the context of the EU eel regulation. The Ministry of Environment of the Republic of Lithuania issued an order of the minister in 2009, to reduce the number of rivers available for the commercial eel fishery by 40% and forbid commercial eel fisheries from using trap nets in lakes. The commercial fishery was banned in the Northern part of the Curonian Lagoon near Klaipėda Strait as a means of reducing mortality among migrating fish. Additional regulations forbidding commercial fishing of silver eels were added in autumn, 2010 and since then eel fishing using traps in rivers and streams is allowed only in spring. Silver eel commercial catches in inland waters (rivers and streams) currently total c. 6100 kg per year (ranging from 2220 to 13081 kg in 2006 – 2016).

Downstream runs of silver eels typically start in autumn and can last until early spring (Bruijs and Durif, 2009). Yet along the South-Eastern Baltic coast, most intense spawning migrations commence during early March and last until late May (Czeczuga and Czeczuga-Semeniuk 2000, Ložys et al., 2008). Autumn migrations are also known to occur during September – October, however these are not as intense as those that occur during spring. According to Ložys et al. (2007) approximately 60% of silver eels start their migration in spring, reducing to 10% during summer and 30% in autumn respectively. Commercial fishing mortality is limited to only two months during spring and is restricted to 46 rivers and streams, but there are no official data regarding the occurrence of poaching which might extend beyond this period, thus the combined impact of commercial fishing and poaching on migrating eel stocks cannot be estimated precisely. Current commercial eel catches in the Lithuanian part of the Curonian Lagoon are negligible (872 kg in 2016) when compared to the approximately 124 tonns per year taken during 1960–1980 (Fig. 2).

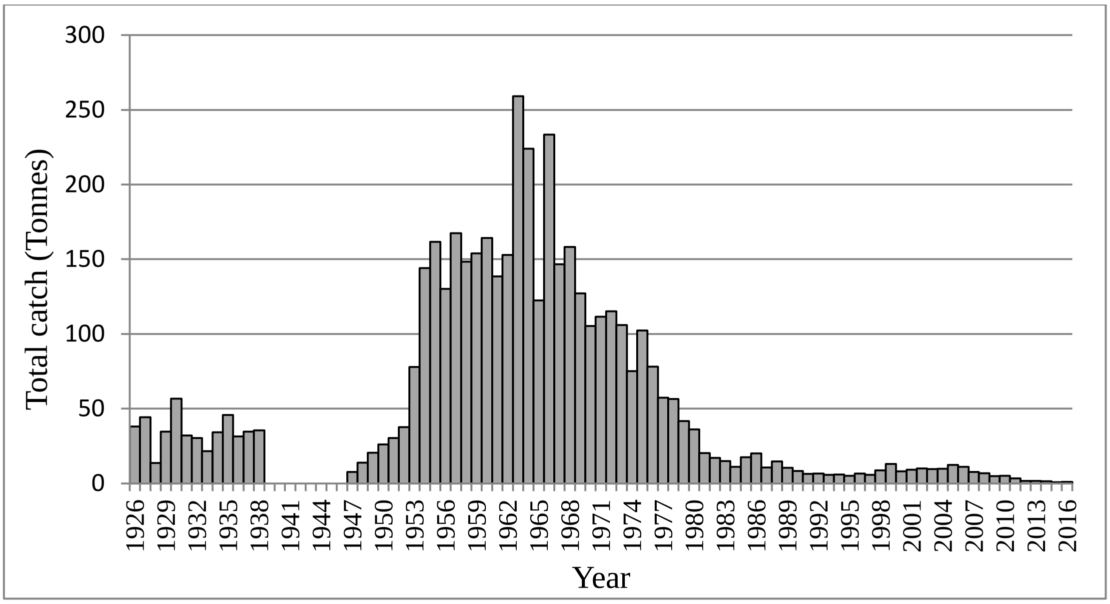

Fig. 2. Commercial eel catches (in tonnes) in Curonian Lagoon (Lithuanian area) during 1926–2016.

As adult eels move downstream they may encounter in-stream barriers, in particular hydroelectric dams which can affect their migration in three ways. First, eels may experience migration delays in the upstream reservoirs as they search for a downstream outlet (Haro et al., 2000; Legault et al., 2003; Behrmann-Goel and Eckmann, 2003). Secondly, while eels search for a downstream passage route, they can become impinged and suffocate on hydropower-plant (HPP) intake screens (Boubée et al., 2001; Amaral et al., 2003; Watene and Boubée, 2005). Finally, if eels are entrained into the HPP turbine intakes, they are exposed to turbine-induced injuries or direct turbine mortality. According to official data, available in the Cadastre of rivers, lakes and ponds of Lithuanian Republic, there are 98 HPPs operating currently and only 24 of them have fish ladders originally designed for salmonid upstream migration. None of the HPP are equipped with special guidance structures for migrating eels. The majority (N=67, 68%) of the 98 HPPs built on Lithuanian rivers use Kaplan turbines, in common with the rest of the Europe (Bruijs and Durif, 2009). According to Larinier and Travade (2002) the typical range of mortality rates is between 15% and 30% in large low-head Kaplan turbines, and from 50% to 100% in the smaller turbines used in most small-scale hydropower plants (Monten, 1985; Hadderingh and Baker, 1998). Some Lithuanian rivers (e.g. Šventoji, Dubinga) that are relatively important for downstream migrating eels are dammed with HPPs that have cross-flow CINK turbines. To my knowledge, no detailed evaluation of mortality rates and injuries to migrating eels caused by cross-flow CINK turbines have been previously reported. Studies on mortalities of other fish species indicate that even small adult and juvenile fish passing through cross-flow turbines suffer mortality rates up to 75% (Gloss and Wahl, 1983, DuBois and Gloss, 1993), which is significantly higher when compared to Kaplan turbines. Therefore a detailed evaluation of eel mortalities in CINK turbines is highly important.

Moreover, Pedersen et al. (2012) reported that some of the eels they tagged with acoustic transmitters spent a few weeks moving in and out of the power canal before finally passing through or disappearing. They concluded that within the study period, only 23% of the tagged eels reached the tidal limit of the destination estuary, mainly due to difficulties in passing the hydropower dam.

Despite numerous studies on eel mortality during passage of various HPPs (mostly Kaplan), there are few data available on eel downstream migration speed in unimpeded rivers (Simon et al., 2011; Bultel et al., 2014; Stein et al., 2016) and lagoons (e.g. Amilhat et al., 2008, Charrier et al., 2012). Previously reported migration rates in regulated rivers have been highly variable, ranging in displacements of between 17.3 (Klein Breteler et al., 2007), 29.4 (Breukelaar et al., 2009), 53 (Verbiest, et al., 2012) and 64.8-93.6 $km \cdot day^{-1}$ (Tesch, 1994). Data on eel migration speed in free flowing rivers are scarce, but Simon et al. (2011) reported mean migration speeds for different eel groups that varied between c. 5 and 70 $km \cdot day^{-1}$, while Bultel et al. (2014) reported a mean migration speed of 4.5 $km \cdot day^{-1}$. There is some evidence that the migration process of European eels in large rivers is discontinuous and that in very large rivers eels may need more than one migratory season to reach the sea (Stein et al., 2016) and may even revert to a non-migratory life stage (Durif et al., 2003; 2006). Moreover, due to their geographical position, Lithuanian rivers are different in terms of hydrobiological conditions, temperature and flow regime compared to rivers in Western Europe, therefore it’s very important to investigate and identify the main patterns of silver eel migration in the North-Eastern region of their distribution range.

More detailed literature reviews regarding eel mortality during downstream migration and migration patterns are presented in the papers “Mortality of Silver Eels Migrating Through Different Types of Hydropower Turbines in Lithuania” (Paper II) and “Silver eel, *Anguilla anguilla* (Linnaeus, 1758), migration patterns in lowland rivers and lagoons in the North-Eastern region of their distribution range” (Paper III).

2. MATERIALS AND METHODS

This section gives a brief overview of the most important methods used within framework of this thesis. More details are given in each publication, respectively (Paper I-IV).

2.1 Laboratory experiment on eel survival

The effect that ongrowing eels in an aquaculture facility had on their survival after transition to *Chironomus* spp. larvae instead of artificial food was tested during three sequential 30–day laboratory experiments. The experimental treatments were: Glass eels (Group A), eels on-grown in an aquaculture facility for 42 days using an artificial diet (Group B) and eels on-grown in an aquaculture facility for 196 days using an artificial diet (Group C). Eels were reared in an experimental system which consisted of ten 240 litre experimental semi-square tanks connected to a mechanical and biological filter. All environmental conditions (light, temperature, concentration of ammonium, nitrite and dissolved oxygen) were equal in all experiments. During the experiments water temperature was maintained at 18.3 ± 0.4°C. Concentrations of ammonium and nitrite were <0.05 mg L^{-1} and the average concentration of nitrate was 13.2±11 mg L^{-1} for the duration of all experiments. Eels were fed *ad libitum* with live *Chironomus* spp. larvae. To evaluate differences between different experiments, specific growth rates (SGR) of each replicate were calculated in addition to mortality rates (M). At the conclusion of experiment with Group C it was evident that weight loss and poor physical condition prevailed among some individuals, although not to the point of obvious morbidity. To allow time for these eels to regain condition this experiment was extended for 30 additional days (Group C_1).

As survival data were non-normal (Shapiro–Wilk's W tests, $p<0.05$), both non-parametric and parametric approaches were used to test for group effect

(A, B, C) on eel survival after one month in laboratory conditions. Kruskal-Wallis ANOVA was followed by Multiple Comparison tests of mean ranks, and One-Way ANOVA performed on arcsine-transformed data was followed by Tukey HSD post-hoc tests.

2.2 Eel mortality in CINK and Kaplan turbines

2.2.1 Large Kaplan turbine. To assess mortality rates of eels migrating downstream through large Kaplan turbines installed at the Kaunas HPP, 25 silver eels were released into the Kaunas water reservoir near the Kaunas HPP intake. These eels prior to release were tagged with Vemco V9 and V13 acoustic tags. This method has been previously used to successfully tag silver eels (Westerberg et al., 2007, Béguer-Pon et al., 2014) without causing increases in mortality rates (Winter et al., 2005; Heupel et al., 2007).

Four VR2W receivers were installed in the area of Kaunas HPP water intake to detect eels entering turbines; four receivers were installed just below the Kaunas HPP to detect eels that had passed through the turbines and four additional receivers were installed on the navigational buoys within the Nemunas Delta.

To locate eels that had passed through the Kaunas HPP but had become possibly lethally injured, a section of the Nemunas River 25 km below the HPP was scanned with two VR2W receivers installed on an inflatable boat prior to the end of transmitter’s estimated battery life.

2.2.2 Small CINK and Kaplan turbines. Eel mortality in the small CINK (Bagdononys HPP and Pabradė HPP) and Kaplan turbines (Valtūnai HPP) was assessed from eels tagged with 12 mm passive integrated transponders (PIT tags). Eels migrating downstream were captured above each HPP using a fyke net and fitted with the tags. After recovery the tagged eels were translocated approximately 2 km to Bagdononys and about 2.5 km to Pabradė

HPPs and using the guidance system described by Oliveira and Pressiat (2011) they were released as close as possible to the turbine's water intake pipe. This release strategy aimed to avoid losses of tagged eels above the HPP due to caseation of migration or predation.

The Valtūnai HPP does not have a water reservoir above the dam wall, thus tagged eels were released just below the site of capture - approximately 800 meters from the HPP.

Following eel passage through the turbine they were recaptured below the HPP in a fyke net.

Eel mortality rate was calculated as the ratio between the number of tagged eels that passed through the turbines and the number of eels which survived without suffering lethal injury.

As the data for eel length, weight and FCF was non-normally distributed (Shapiro–Wilk's W tests, $p<0.05$), the non-parametric Mann-Whitney test was used to test for the effect of length on eel survival during passage through the turbine, and choice of migration route through turbine or fish ladder (at Valtūnai HPP only), as well as the effects of length and weight on migration success from Kaunas HPP to the Nemunas Delta.

2.3 Eel migration patterns and migration success

A total of 63 silver eels were caught in four rivers in Eastern Lithuania during their spawning migrations and tagged with Vemco acoustic tags during spring and autumn 2014. Migration was studied in four rivers: the Neris, Siesartis and Žeimena in which they could migrate freely downstream, and the Nemunas in which eels had to pass through a HPP. Eels that successfully performed downstream migration were detected with receivers installed in the Nemunas Delta (N = 4) and Klaipėda Strait (N = 4). To locate missing eels, downstream of the eel release sites in the Neris, Žeimena and Siesartis Rivers and a 25 km section of the Nemunas River below the Kaunas HPP were scanned two months before the end of the estimated duration of transmitter batteries, with VR2W receivers installed on a boat drifting downstream. In addition, Žeimenys Lake was scanned in case tagged eels had migrated upstream from the Žeimena River.

Migration success (MS, %) of the tagged eels was calculated according to the formula:

$$\boldsymbol{MS = (N \div N_t) \times 100}$$

Where: N – number of tagged eels detected by acoustic receivers (in the Nemunas Delta and/or Klaipėda Strait); N_t *– number of all tagged eels.*

MS for eels released upstream the Kaunas HPP was calculated only for eels which had passed the HPP. The fate of eels did not detected in the Nemunas Delta or Klaipėda Strait remains unknown; these eels were omitted from analysis of the migration speed.

The speed of long term downstream migration (V_{long}) was calculated as time spent to cover the distance between the release site and the receivers installed in the Nemunas Delta or in the Klaipėda Strait and expressed as km·day^{-1}. The speed of transient migration (V_{tran}) was calculated in the Nemunas Delta and Klaipėda Strait as the time lag between the first detection of a tag by the first and last receivers (5 km distance in the Nemunas River and 4.6 km in the Klaipėda Strait).

Data for eel migration speed, FCF and the distance between the release site and the Baltic Sea were not normally distributed (Shapiro–Wilk's W tests, $p<0.05$), the non-parametric Mann-Whitney test was used to test for differences in parameters between the eels released in to dammed (Nemunas) and free-flowing rivers. Simple linear regression was used to test the effect of distance of release site from the Sea, eel length, river slope and K on the speed of downstream migration. Fisher's exact test was used to test eel MS differences between dammed, free-flowing rivers and the Curonian Lagoon.

2.4 Accumulated energetic reserves and swimming potential

In total 114 eels were collected from 10 different rivers in the Eastern and Southern parts of Lithuania for the study. Migrating eels were caught by a fyke net during April–November in 2013–2015. Morphometric measures (total body length and weight; gutted weight; height and width of the eye; length of the pectoral fin; and the weight of liver, gonads and emptied gut) were made immediately after anaesthesia on the fresh fish. The silvering stage of sampled eels was determined as described by Durif et al. (2009). A section of the lateral muscle from both sides of the body, 2.5 cm away from the anal vent, was removed for the analysis of muscle fat content (the total lipid content of the muscle) using a method described by Anderson (2004). Swimming potential was calculated according to van Ginneken and van den Thillart (2000). The distance of migration from eel capture place to the spawning area in the Sargasso Sea was estimated to be c. 7900 km based on Clevestam et al. (2011).

Relationships between the silvering stage and fat content were determined using correlation analysis. As only 7 male individuals were caught (SMII), the correlation analysis was conducted on a dataset of undifferentiated and female eels (SI–SFV). Pearson’s correlation test was used and silvering stage variable was log-transformed. One-way analysis of variance (ANOVA) was followed by generalised Tukey’s HSD post-hoc tests to indicate homogenous stage groups.

3. RESULTS

Only the main results are presented in this section. Detailed results are given in each publication, respectively (Paper I-IV).

3.1 Laboratory experiment on eel survival

Average initial weight of Group A was 0.46 ± 0.01g (N = 400), while the weight of Group B and Group C was 1.14 ± 0.1 g (N = 100) and 8.31 ± 1.9 g (N = 100) respectively. Although the absolute average growth rate (abs) of Group A (abs 0.13 ± 0.02 g) was lower than Group B (abs 0.19 ± 0.1 g) over 30 days, however, its relative growth rate (rel) as a proportion (%)of initial weight (rel 26.2 ± 5.9%; SGR 0.8 ± 0.1) was higher than Group B (16.8 ± 8.6%; SGR 0.5 ± 0.2). In contrast, both absolute and relative growth rates of Group A were larger that Group C (abs -0.5 ± 0.7 g; rel -5.9 ± 7.7%; SGR -0.2 ± 0.3).

Survival within the first 30 days after transfer from aquaculture to experimental conditions differed significantly between Group A and B as well as between Group B and C. Group A had 100% survival compared to 13% and 1% mortalities for Groups B and C respectively at the end of their 30-day laboratory periods. There were no statistically significant differences in survival rates between Group A and C during the 30-day experimental periods.

After the 30-day period of the experiment with Group C the mortality rate was negligible (only 1 individual died), but weight decreased by 0.5 ± 0.7 g per eel. Accordingly, this experimental treatment was extended for an additional 30 days (Group C_1). After additional 30 days the mortality rate of the eels increased and substantially varied among tanks (15.0 ± 20.1%) yet with a weight gain per surviving eel of 0.6 ± 1.1 g (7.6 ± 12.5% of initial body weight; SGR 0.2 ± 0.4). All mortalities in Group C_1 occurred within the first 11 days of the second phase with none thereafter. The total mortality rate after the first and second phases of the experiment was estimated to be 16%, which is similar to the mortality rate observed for Group B.

3.2 Eel mortality in CINK and Kaplan turbines

3.2.1 Small CINK turbines. All 52 eels released upstream from Bagdononys HPP passed the turbine immediately after release and were recaptured below the HPP. All eels suffered lethal injuries causing 100% mortality.

Out of 26 eels guided to the Pabradė HPP water intake pipe none were recaptured below the HPP.

3.2.2 Large Kaplan turbine. Out of 25 eels released upstream of the Kaunas HPP water intake area, 21 (84%) moved downstream through the turbines and were detected below the HPP. Four eels did not migrate downstream and remained in water reservoir until the end of transmitter battery lifespan. Eleven eels (52.4%) were detected in the Nemunas Delta (212 km downstream from Kaunas HPP). Transmitters showed that five eels (23.8%) remained stationary in close proximity to the Kaunas HPP (from 0.5 km to 6.2 km) until the battery was discharged. As a consequence it was concluded that these eels had died. The fate of the remaining five eels after passing through the HPP turbines remains unknown because the transmission signal ceased between the scanned sector of 25 km downstream HPP and the Nemunas Delta.

3.2.3 Small Kaplan turbine. Following release, all tagged eels (N=64) passed the Valtūnai HPP during the same night. Forty two eels (66%) migrated through the turbine, while the remaining 22 eels (34%) were caught after passing through the fish ladder. Eels caught passing through the fish ladder were significantly larger (p<0.001, mean TL=72.0±7.2 cm, W=681±188 g) than eels passing directly through the turbine (mean TL=66.1±6.4 cm, W=476±109 g); their FCF was also significantly larger (p<0.001, mean

FCF=0.18±0.02) when compared with eels passing directly through the turbine (mean FCF=0.16±0.02). Eel mortality in the Kaplan turbine at Valtūnai HPP was estimated to be 52.4% because 22 out of 42 eels suffered lethal injuries while passing through the turbine.

There were no significant differences (p>0.05) in mean length, weight and FCF between eels that suffered lethal injuries (N=22; TL=67.3±7.6 cm, W=494±131 g, FCF=0.16±0.02) and those which passed through the turbine successfully (N=20; TL=64.8±4.5 cm, W=458±77, FCF=0.17±0.01).

3.3 Eel migration patterns and migration success

In total, twenty two out of 63 silver eels released into rivers of Eastern Lithuania were never detected post-release, consequently their fate is unknown. The remaining 31 eels successfully migrated downstream and reached the Nemunas Delta; MS = 49%. Mean V_{long} (± SD) of these eels was 11.7 ± 11.1 $km \cdot day^{-1}$. There were no significant differences (p>0.05) in mean length, K and the distance from the release site to the Baltic Sea between eels that reached the Nemunas Delta and those which apparently did not.

Eighteen out of 38 silver eels released into free-flowing rivers (Neris, Žeimena and Siesartis) of Eastern Lithuania were never detected post-release, consequently their fate is unknown. The remaining 20 eels successfully migrated downstream and reached the Nemunas Delta; MS = 53%. Mean V_{long} (± SD) of these eels was 10.7 ± 10.7 $km \cdot day^{-1}$.

Out of 25 eels released upstream of the Kaunas HPP, 21 (84%) moved downstream through the turbines and were detected below the HPP. Twelve eels migrated within 24 hours after release, while nine eels delayed passing through by one to 47 days. Four tagged eels did not migrate downstream and stayed in the Kaunas Reservoir until at least when the transmitter battery became discharged. Their fate remains unknown. Out of the 21 eels which migrated through the HPP, 11 were detected in the Nemunas Delta (MS = 52.4%). Mean V_{long} (± SD) of these eels was 13.6 ± 12.0 km·day^{-1}.

Most of the tagged eels (N = 54, 86%) were released during late May - early June and nine eels (14%) were released in September. In total thirty-one eels (49.2% of all eels released) were detected migrating through the Nemunas River Delta: one eel (3%) arrived in May, five eels (16%) in June, eight (26%) in July and one (3%) in September. The majority (N = 15, 49%) were detected in October and the one (3%) was detected in November.

V_{tran}, estimated within the Nemunas Delta was 67.2 ± 39.9 km·day^{-1} which was significantly ($p<0.05$) higher compared to V_{long} in rivers.

Scanning in smaller rivers (Neris, Žeimena and Siesartis), adjacent lake and section of Nemunas River below the Kaunas HPP did not result in detection of any eels, so the fate of 32 tagged eels (51%) remains unknown.

Out of 31 eels, which were detected entering the Curonian Lagoon, at least four (13%) were caught by fishermen. Until the end of transmitter battery operation, 22 eels (MS = 71%) were detected in Klaipėda Strait prior to entering the Baltic Sea, while the fate of the remaining 5 eels (16%) remains unknown. The mean V_{long} in the Lagoon was estimated to be 14.6 ± 16.9 km·day^{-1}. V_{long} (in the rivers, in the Lagoon and total (rivers+lagoon)) was not significantly correlated with distance of the release site from the Baltic Sea, river slope, TL or FCF. Also, there was no significant difference ($p>0.05$) between the mean V_{long} in rivers (11.6 ± 11.1 km·day^{-1}) and the Curonian Lagoon (14.6 ± 16.9 km·day^{-1}).

The V_{tran}, estimated in the Klaipėda Strait was 35.6 ± 25.79 km·day^{-1}. There is no significant differences ($p>0.05$) between mean V_{tran} in the Nemunas Delta and in the Strait, however V_{tran} was significantly ($p<0.05$) higher compared to V_{long} in rivers and in the Lagoon.

The peak period of eels entering the Baltic Sea was observed during late fall: 18 eels (82%) were detected in the Klaipėda Strait during October-November while the remaining four eels were detected once each in June, July, December and January, respectively.

3.4 Accumulated energetic reserves and swimming potential

The majority of eels sampled (65.8%, N = 75) were at the last silvering stage (SFV for females or SMII for males), whereas eels of stage SFIV accounted for 10.5% (N = 12). The yellow eels (stages SI, SFII and SFIII) accounted for 23.7% (N = 27) of all eels sampled.

Migrating male eels of the latest SMII silvering stage had the highest muscle fat content, varying from with their swimming potential varying from 7987 to 8462 km (8152 ± 174 km, mean ± SD), while the females of the latest (SFV) silvering stage had an average fat content of 26.3 ± 3.7 with average swimming potential of 6743 ± 1116 km. Eels at silvering stage SFIV had an average fat content of 26.3 ± 2.7%. The average swimming potential of these eels was equivalent to 6798 ± 976 km. The yellow eels possessed lower percentages of fat content – SFIII and SFII eels had 25.1 ± 2.8 and 17.6 ± 4.6% average fat content, respectively. The yellow eels at the silvering stage SI had the lowest fat content (average 4.6 ± 1.9%).

The analytical results indicated that 100% (N = 7) of male eels and 30.9% (N = 21) of female eels at the latest silvering stages (SMII and SFV, respectively) possessed sufficient fat reserves to be capable of migrating to the Sargasso Sea (>7900 km). The remaining 69.1% (N = 47) of the female eels at stage SFV had insufficient energy resources to complete the migration. Four out of 12 (33.3%) eels sampled at the silvering stage SFIV had sufficient energy resources for spawning migration.

4. DISCUSSION

Recognition of the dramatic downward trend in European eel recruitment since the 1980s has led to numerous attempts to drive stock recovery forward throughout Europe (ICES, 2011). Recovery measures differ among member states of the European Union but are united by the aim of recovery of the eel stock. To reach the targeted 40% spawner escapement, relative to the best possible estimate of spawner biomass in a pristine state, the Lithuanian Eel Management Plan mainly relies on an extension of stocking programme (Ložys et al., 2008). Since the Lithuanian EMP was approved by European Commission in 2009, intensive eel stocking of inland water bodies started. However, little is known about possible ongrowing effects on European eel growth and survival after stocking (ICES, 2015b). The results of the laboratory experiment on eel survival suggest that after 30 days, there is no significant difference in survival rates between glass eels (Group A) and eels on-grown for 196 days (Group C), even though the survival rate of eels on-grown for 42 days (Group B) is significantly lower. However, the SGR in the experimental group C after the initial 30 day period was negative indicating weight loss and poor physical condition among some individuals, while in all other experimental groups SGR was positive, indicating that these eels were able to gain weight on the *Chironomus* spp. diet. Chironomids were reported to be one of the main food items found in the eel's stomachs, even when the abundance of larvae in the lake was low (de Nie, 1982). After the additional 30 days of experiment with Group C, their survival rate decreased by an additional 15%, even though the SGR of surviving individuals increased and became positive (Group C_1). Kearney et al. (2011) suggest a link between initial energy reserves in the shortfin glass eel (*A. australis*) and its survival in captivity. This might explain the performance of the eels in the experiments: the largest eels were well-nourished in the aquaculture facility and had accumulated enough energy reserves to cope with impaired ability to adapt to feeding on *Chironomus* spp. or insufficient food intake during the first 30 days, thereby delaying the increase in mortality that was observed during the beginning of the second phase of the experiment. Considering the results of the current study and similar findings in field studies (Pedersen, 2000; Wickström, 2001; Simon and Dörner, 2014; Pedersen and Rasmussen, 2016), it could be argued that eels should be stocked as soon as possible after capture, or kept under aquaculture farm conditions for the shortest duration feasible and fed or at least weaned with natural food prior to release to improve their ability to adapt to the natural conditions found in the wild.

After stocking, eels spend several years or even decades in fresh or brackish waters before reaching the silver eel stage and commencing their spawning migration, which is time-dependent and generally takes place during spring and autumn. The practice of stocking eels in Lithuania persisted for many decades, but the motivation was direct enhancement of commercial or recreational fishing success without aiming to facilitate migration to spawning areas to improve population recruitment. Consequently, there was less concern when eels were often stocked above HPPs or dams, despite the substantial mortality that can occur during downstream migrations which will dramatically reduce the number of spawners (Adam and Bruijs, 2006; Winter et al., 2006; 2007; Bruijs and Durif, 2009; Aarestrup et al., 2010) or delay in their spawning migration (Legault et al., 2003). The current study demonstrated that eel migration through small cross-flow CINK turbines results in a 100% mortality rate as all eels used for the field experiment suffered lethal injuries. Nevertheless, mortality rates can be significantly reduced if a fish ladder is available for downstream migrating eels to bypass HPP, as demonstrated in this study. Even though, eels were reported to use fish passes, originally designed for upstream salmonid migration, sporadically (Jansen et al., 2007; Verbiest et al., 2012), the results of the current study suggest that 34% of the eels migrating downstream in the Siesartis River passed through the fish ladder uninjured, in contrast to the 66% of eels observed passing through Kaplan turbines that suffered a 52% mortality rate. Eels caught passing through the fish ladder were significantly larger compared to those caught passing directly through the turbine. This is presumably arose because of the protective 35 mm metallic screens at the HPP water intake zone which prevent larger eels from entering the turbine. Nonetheless, the results of this study suggest that this screening method is insufficient for the protection of all migrating silver eels as c. two thirds of eels pass directly through the turbines resulting in an overall high mortality rate. ICES (2007) recommends that small male silver eels require bar intervals <9mm for protection, whereas females may be prevented from entering turbines by bar intervals <15mm. The effectiveness of a protective screen with a bar interval of c. 10 mm installed in the water intake pipe was also demonstrated in the current study, as none of 26 eels guided into the Pabradė HPP water intake pipe were recaptured below the HPP. This protective screen was not included in the initial HPP construction design and could not be reasonably known in advance of this study. Its presence was only discovered after the field experiment during attempts to identify reasons for the ‘disappearance’ of all tagged eels guided into the intake of the turbine. This implies that effective screening in the absence of a fish ladder or other effective way for eels to bypass turbines will cause cessation of eel migration, as eels either would be impinged in the screen or unable to find a way to continue their migration.

As was suggested previously, mortality in the large Kaplan turbines at the Kaunas HPP was found to be lower compared to mortality rate in small turbine at the Valtūnai HPP. Out of 21 eels which passed the Kaplan turbines in the Kaunas HPP, 5 eels (23.8%) were detected to be stationary below the HPP until the tag transmitter’s battery expired, indicating that the possibility that they remained alive was negligible. The fate of the other 5 eels, which disappeared somewhere between the scanned sector 25 km downstream of the HPP and the Nemunas Delta remains unknown, however it has been suggested that some migrating eels cease their migration for lengthy periods (Winter et al., 2006; Aarestrup et al., 2010). Durif et al. (2003; 2006) suggest that in very large rivers, eels may need more than one migratory season to reach the Sea and may revert to a non-migratory life stage, thus it is likely that those eels detected well downstream of the HPP survived.

It has been reported that eels may experience migration delays in water reservoirs as they search for a downstream outlet (Larinier and Travade, 1999; Haro et al., 2000; Behrmann-Goel and Eckmann, 2003; Legault et al., 2003) and therefore migration becomes extended in time. Results of the current study partly support this observation as 36% of the eels released upstream from the Kaunas HPP also delayed passing through the turbines for periods from one to 47 days, while 16% of eels did not migrate at all.

Moreover, not all eels that were migrating in unimpeded rivers or free-flowing river sections (Neris, Žeimena and Siesartis) successfully reached the Nemunas Delta before their tag transmitter batteries had fully discharged. Mean downstream migration speed and escapement success were almost the same in the shorter 210 km Nemunas River (53%, 10.7 km·day^{-1}) where eels were exposed to the negative HPP effect as compared to the considerably longer 300–480 km free-flowing rivers (52.4%, 13.6 km·day^{-1}). Overall eel migration success from Lithuanian inland waters was calculated to be 49% with a mean migration speed of 11.7 km·day^{-1}. During downstream migration the eels were not exposed to commercial fishing (except in the Lagoon) because they were all released downstream of licensed fishing sites. The impacts of predation, recreational angling, poaching or other sources of mortality are nevertheless unknown. Scanning with boat-based receivers in the rivers, an adjacent lake, and the section of Nemunas River below the Kaunas HPP did not result in detection of any eels. Presumably the missing eels were either caught by anglers or predators and their tags were taken away from the river, or the eels stayed somewhere in the Nemunas River below the scanned reaches, or perhaps entered small tributaries of the main rivers and were missed during active scanning. Thus migration success is likely to be higher if some eels resumed migration after their transmitter batteries had expired.

Relatively low migration speeds observed in the current study might be related to seasonal differences among eel spawning migrations, as along the South-

Eastern Baltic coast, most intense spawning migrations start during early spring (Ložys et al., 2008), whereas downstream runs of silver eels in Western Europe typically start during autumn (Bruijs and Durif, 2009). The earlier commencement of downstream migration has led to an assumption that eels enter the sea earlier as a consequence, but the results from the current study demonstrated that a majority of migrating eels caught in streams during spring did not enter the Baltic Sea until late autumn (October-November). Despite the similarity between the migration speed in the Curonian Lagoon (14.6 km·day^{-1}) to that in rivers, migration success was significantly higher (71%) in the Lagoon. Relatively high migration success in the Lagoon might also be explained by eels reaching the Lagoon at the end of the continental migration phase and, as suggested by Righton et al. (2016), had adopted a rapid migratory strategy, such that most of these eels (N=22) did not cease their migration through the Lagoon. Migration strategies of the four eels caught by fishermen in the Lagoon and the five eels whose fate is unknown (they might also have been caught but not reported) remain unclear.

After downstream migration most eels enter Baltic Sea during late fall (October-November) and presumably continue migrating to the Sargasso Sea spawning grounds. Migrating silver eels at the final silvering stage do not feed (Tesch, 2003); instead they completely rely on accumulating sufficient fat stores during the sedentary yellow eel stage spent in coastal or inland waters to obtain energy for migration and gonad development (Tesch, 2003). Previously it was reported that eels of stocked origin might have insufficient muscle fat reserves (Couillard et al., 2014. However, in contrast to previous observations, results of the current study suggest that at least 37% of silver eels of stocked origin at the final silvering stage (SFV and SMII) have accumulated sufficient energetic stores of fat for gonadal development and spawning migration of c. 7900 km to the Sargasso Sea. The remaining 63% of eels at the final SFV and SMII silvering stages had insufficient fat stores, with an average shortage of 2.5 ± 0.9%. Four out of 12 eels at the SFIV silvering stage had enough energetic resources to reach the spawning grounds, while the remaining eight eels were unable to successfully undertake the spawning migration due to insufficient stored energy. However, some eels at silvering stages SFV and SFIV were found to be feeding during downstream migrations (Dainys, unpubl. data; Westin, 2003), thus these eels are possibly able to augment their stored energetic resources. The remaining 27 eels were described to be in the yellow (SI, SFII or SFIII) eel stage with relatively low fat content (18.4 ± 9.3%). Swimming potential of these eels was not calculated because downstream movements of these eels might have been linked to local movements rather than actual spawning migration (Ovidio et al., 2013; Cobo et al., 2014).

Overall, the results of the current study suggest that aiming to achieve the best results while implementing the National Eel Management Plan, eels should be stocked as soon as possible after their capture in the wild or at least kept under aquaculture conditions for the shortest duration feasible. In addition, they should be fed or at least weaned with natural food before their release. After these stocked eels reach silver eel stage and start their downstream migration, substantial mortality occurring during their downstream migration can dramatically reduce the number of spawners when releases occur upstream of the HPP. Eel stockings should be carried out in water bodies which are not upstream HPP. If due for some reason stocking must be performed upstream of HPP, then a fish ladder in combination with effective screening must be installed to reduce HPP induced eel mortality. Even though eels stocked into Lithuanian waters were shipped by plane for more than 2000 km prior to stocking and had no chance to imprint the entire route from the Sargasso Sea to the stocking area, 37% of the silver eels performing downstream migration accumulated sufficient energetic stores of fat needed for gonadal maturation and migration to the spawning grounds. The remaining 63% of the silver eels had a marginal shortage of energy resources and were likely to increase their muscle lipid content to an adequate level for successful migration. These losses should be factored into any assessment of eel management in Lithuania.

5. CONCLUSIONS

1. On-grown eels have no advantage in survival compared with glass eels when fed *Chironomus* spp. in the laboratory. Likely explanation is that eels must switch their diet from artificial to natural food, a transition to which at least some on-grown eels appear unable to cope.
2. A CINK turbine was found to be causing lethal injuries resulting in 100% mortality of eels passing into it, whereas Kaplan turbines caused significantly lower mortality rates.
3. One third of eels migrating downstream on river impeded by HPP used fish ladder, originally designed for upstream migration of salmonids. Therefore, the installation of fish ladders, especially in combination with effective screening, may be a measure that effectively mitigates some of the impact of HPPs by reducing anthropogenic mortality rates during migration.
4. Almost a quarter of all eels engaged in downstream migrations were at the yellow eel stage.
5. Overall eel migration success in Lithuanian rivers and the Curonian Lagoon was 35%. The average estimated migration speed was 11.7 km d^{-1}in rivers, and 14.6 km d^{-1} in the Curonian Lagoon.
6. The peak period for eels entering the Baltic Sea was observed during late fall.
7. More than one third of silver eels across all stages that had been previously translocated for a considerable distance before their subsequent release into inland waters of the North-Eastern region of their distribution range for restocking natural populations, had sufficient energetic resources for successful spawning migration and gonadal maturation. The remaining two thirds of silver eels had marginal shortages of energetic reserves, but when engaged in downstream migrations these eels were possibly able to feed to increase the fat reserves stored in their muscle tissue.

8. RECOMMENDATIONS

1. Considering the results of the survival study and similar findings in field studies, it is recommended that eels should be stocked as soon as possible after capture, or at least kept under aquaculture conditions for the shortest duration feasible. In addition, they should be fed, if possible, using natural food to improve their ability to adapt to the natural conditions found in the wild.
2. Seeking for the highest silver eel production escaping to the Sea, the stocking of eels should be carried out in water bodies which are not impeded by HPP’s, regardless of whether or not the HPP have a fish ladder installed.
3. Cross-flow CINK turbines were found to result in 100% mortality of passing eels. Therefore, replacement of these turbines with more fish-friendly models is crucial. Fish ladders provide a way for migrating eels to get around existing HPP’s and in this way reduce the mortality of eels migrating downstream. Therefore, the installation of new fish passes in combination with effective screening is essential in ensuring that restocking strategies are not inefficient.

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ORIGINAL ARTICLE

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Do young on-grown eels, *Anguilla anguilla* (Linnaeus, 1758), outperform glass eels after transition to a natural prey diet?

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Summary

Survival rates among European eels, *Anguilla anguilla* (Linnaeus, 1758), on-grown using a formulated diet in a commercial aquaculture facility, were compared with glass eels from the same cohort following their transition to a natural prey diet in the laboratory. Treatments included zero, 42-day, and 196-day periods of grow-out prior to 30-day experimental periods when eels were fed *Chironomus* spp. larvae (10 tanks, each containing 240-L water and 40 glass or 10 on-growing eels; 12:12 hr photoperiod; water temperature 18°C). All glass eels survived, compared to 87% (42-day) and 99% (196-day) for on-grown eels. Although the eels on-grown for 196 days had a high survival rate, they did lose weight. Farm-reared eels may have accumulated sufficient resources over the 196-days to survive the first 30 days after weaning from a formulated diet, but not for an additional 30 days (84% survival). Lack of superior survival rates among on-grown eels challenges the presumed benefits of releasing on-grown eels for population restoration.

1 | INTRODUCTION

Rapid population declines have been observed since the 1980s over the entire distribution range of the European eel (*Anguilla anguilla* L.; Dekker, 2004; Feunteun, 2002; ICES, 2015; Moriarty & Dekker, 1997). As a consequence, in 2007 the European Union (EU) issued the Regulation of European Council No. 1100/2007, which lays down measures for the restoration of European eel stocks. This regulation obliges member states to develop and implement national Eel Management Plans. The aim of these plans is to allow 40% of spawners (silver eels) from a pristine stock to migrate towards the spawning area in the Sargasso Sea; restocking inland waters is one means to accomplish this (Dekker & Beaulaton, 2015). Nowadays, after capture in the wild, glass eels are often on-grown in aquaculture facilities prior to translocation and release. During the on-growing phase, eels are weaned from a natural diet and fed with specially formulated food. Their weight increases up to 10-fold during this period; consequently, mortality among on-grown eels released back into the wild was believed to be lower when compared to mortality rates among eels liberated at the glass eel stage. This construct is speculative and in need of testing (ICES, 2007, 2015). Moreover, there is evidence that stocking of hatchery-reared fish does not always deliver significant improvements (Blaxter, 2000; Larscheid, 1995). White and Knights (1994) suggested that any initial growth advantage from releasing on-grown eels is lost after about 5–6 years. Simon and Dörner (2014) found over a 7-year study period following re-stocking, that glass eels exhibited superior growth and condition compared to eels on-grown in an aquaculture facility, and had caught up in body size within 3–4 years post-release. There is also evidence that stocking with on-grown eels may result in poorer survival rates than for glass eels (Berg & Jørgensen, 1994; ICES, 2007; Pedersen, 2000; Wickström, 2001). Exposure of different fish species to an artificial environment during on-growing can produce phenotypic changes that give rise to impaired migratory and anti-predator behaviour, thereby reducing chances of survival (Brown & Laland, 2001; Svåsand, 2004). There has also been speculation that on-growing in aquaculture facilities adversely affects the capacity for the weaning of eel to natural food during the post-release period (ICES, 2013; Smirnov, Chebanova, & Vvedenskaya, 1994), resulting in increased mortality. In addition to these negative aspects of farm-reared eels, glass eel on-growing in aquaculture facilities poses risks of spreading parasites and diseases, genotypic population alteration, release of slower growing individuals caused by size-dependent sorting, as well as increasing the cost per stocked eel (Egusa, 1979; ICES, 2011).

To our knowledge, there have been no laboratory studies undertaken to compare survival rates among on-grown European eels and glass eels under controlled conditions. The primary aim of the present study was to test how well on-grown eels could be weaned from a formulated diet to feed on *Chironomus* spp. larvae that are typically consumed by eels in natural water bodies (de Nie, 1982), and how this transition affects their survival in comparison to glass eels under the controlled conditions provided by an indoor laboratory facility.

2 | MATERIALS AND METHODS

The effects of three pre-release options on the survival of translocated wild-caught glass eels were tested during 30-day sequential laboratory experiments when the eels were fed *Chironomus* spp. larvae. These treatments were: Group A, glass eels not on-grown; Group B, eels fed a specially formulated diet whilst on-grown in an aquaculture facility for 42 days; and Group C, fed for 196 days. The experiments were run sequentially to ensure that eels for each treatment were sourced from the same cohort of imported glass eels, to control for inherent differences in growth and survival.

After 30 days in the Group C treatment, it was evident that weight loss and poor physical condition prevailed among some individuals, although not to the point of obvious morbidity. To allow time for these eels to regain condition, this experiment was extended for an additional 30 days (Group C_1).

2.1 | Source of eels for experimental treatments

Glass eels were shipped from the United Kingdom and upon arrival in Lithuania were transported to an aquaculture facility in the Vilnius district for rearing. Initially, the eels in this facility were fed cod roe at 10% of their body weight for the remainder of the glass eel phase. At the beginning of the post-glass eel on-growing phase the eels were transitioned to a specially formulated fish food (ALLER FUTURA EX, 00-0 GR., http://www.aller-aqua.com/introduction-to-fish-feed/warm-freshwater-species). This meant that prior to the transfer of eels from the aquaculture facility to the experimental laboratories at Lithuania's Nature Research Centre (NRC), the Group A glass eels were fed only cod roe, whereas both the B and C groups of on-grown eels were progressively transitioned and reared exclusively on formulated fish feed. Water temperature in the rearing system at the aquaculture facility was maintained within the range of 25–27°C. Immediately after transportation to NRC, the eels were acclimated to a lower water temperature of 18°C in the laboratory experimental system. No mortality was observed during this acclimation period.

2.2 | Experimental system

Ten experimental semi-square fiberglass tanks (length = 0.6 m, width = 0.6 m and depth = 0.8 m), each containing 240-L water were connected to the same recycling system (mechanical filter Hydrotech drum, USA, mesh size = 40 μm; biological filter Bio-Blok 200, Denmark, volume = 4.5 m^3, biofilter material inner surface = 200 m^2/m^3). The experimental system was exposed to simulated day–night cycles of artificial light (Hagen Sun Glo T8 4200K lamps; 12:12 hr photoperiod). Water flow rate from the filter to each experimental tank was 5 L/min (50 L/min through a biological filter) and monitored twice a day. After gradual adaptation, eels were randomly allocated among 10 replicate tanks each containing 40 individuals in the Group A experiment ($N = 400$), and 10 individuals in each of Group B ($N = 100$) and Group C ($N = 100$). During all experiments the eels were fed ad libitum with live *Chironomus* spp. larvae. Eels in all replicates were fed at the same time and all uneaten larvae were removed within 2 hr after feeding. Throughout the experiments accumulated faeces were removed every 2 days before feeding. Total wet weights of eels within each experiment replicate, i.e., 10 replicates per group, were weighed at the beginning and end of each experiment. Individual measurements were not taken in order to minimise the risk of handling-induced mortality. Weights of a sample ($N = 40$) of individual eels retained in the aquaculture facility were measured periodically and their means calculated over duration of the study. Fish health was monitored in each tank daily; no external symptoms of any diseases were noted during this series of experiments. Tests for ammonium and nitrite concentrations were performed at 2-day intervals and for nitrate at 5-day intervals (Aquamerck Nitrite Test 14658, Aquaquant Ammonium Test 14400; Aquamerck Nitrate Test 11170; Merck, Germany). Samples for water quality tests were taken from outlet pipes of each tank.

2.3 | Data analysis

Specific growth rates (SGR) of each replicate were calculated in addition to the survival rates (S). The SGR was calculated as described in Wootton (1990) and used to monitor eel condition.

As survival data were non-normal (Shapiro–Wilk's W tests, $p < .05$), both non-parametric and parametric approaches were used to test for group effect (A, B, C) on eel survival after 1 month in laboratory conditions. Kruskal–Wallis ANOVA was followed by Multiple Comparison tests of mean ranks, and One-Way ANOVA performed on arcsine-transformed data was followed by Tukey HSD post-hoc tests. Statistical analysis was conducted with StatSoft STATISTICA® 8 software.

3 | RESULTS

During the experiments water temperature was maintained at 18.3 ± 0.4°C. Concentrations of ammonium and nitrite were <0.05 mg/L and the concentration of nitrate was <38 mg/L for the duration of all experiments.

3.1 | Growth

Average initial weight of Group A was 0.46 ± 0.01 g ($N = 400$), while the weighs of groups B and C were 1.14 ± 0.1 g ($N = 100$) and

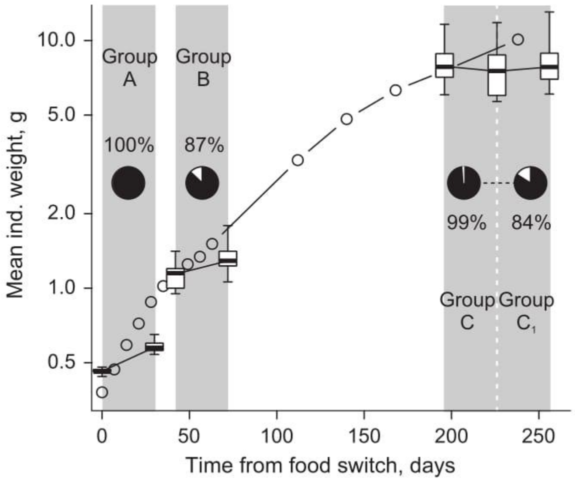

FIGURE 1 Changes in mean individual weight of eels (*Anguilla anguilla*) in an aquaculture facility (open circles) and among different age groups when transferred to laboratory conditions (boxplots: median, quartiles, min-max). Group A eels fed with cod roe, Group B eels raised 42 and Group C 196 days on formulated fish food. Pie charts with percentages = survival for each treatment group (cumulative in 196-day group). The *x*-axis represents total days of on-growing and experimental treatment, amounting to 256 days in Group C_1

8.31 ± 1.9 g (N = 100), respectively. Although the absolute average growth rate (abs) of Group A (abs 0.13 ± 0.02 g) was lower than Group B (abs 0.19 ± 0.1 g) over 30 days, its relative growth rate (rel) as a proportion (%)of initial weight (rel 26.2 ± 5.9%; SGR 0.8 ± 0.1) was higher than Group B (16.8 ± 8.6%; SGR 0.5 ± 0.2). In contrast, both absolute and relative growth rates of Group A were larger that Group C (abs −0.5 ± 0.7 g; rel −5.9 ± 7.7%; SGR −0.2 ± 0.3; Figure 1).

3.2 | Survival

Survival within the first 30 days after transfer from aquaculture to experimental conditions differed significantly between groups A and B as well as between groups B and C (Table 1). Non-parametric and parametric tests gave congruent results. Group A had 100% survival compared to 13% and 1% mortalities for groups B and C, respectively, at the end of their 30-day laboratory periods. There were no statistically significant differences in survival rates between groups A and C during the 30-day experimental periods.

3.3 | Extension of experiment with Group C

The limited duration and sequential conduct of experiments with groups A and B precluded comparison of how each treatment would affect survival over the longer term. Nevertheless, the SGR of these two experimental groups was positive and physical condition was evidently good, suggesting that these eels were feeding and gaining weight in contrast to those in Group C.

TABLE 1 Pair-wise comparisons of survival rates after 30-day experiments among Groups A, B and C

Treatment Group	A	B	C
A	–	**<.001**	.870
B	**.019**	–	**<.001**
C	1.000	**.048**	–

p-values of Tukey HSD tests following One-Way ANOVA ($F_{2,27}$ = 14.1, p < .001) given above diagonal; p-values of Multiple Comparison tests of mean ranks following the Kruskal–Wallis ANOVA ($H_{2,\ N=30}$ = 14.8, p < .001) given below diagonal. Bold = significant probabilities (p < .05).

After the 30-day period of the experiment with Group C the mortality rate was negligible (only one individual died), but weight decreased by 0.5 ± 0.7 g per eel. It was evident that weight loss and poor physical condition prevailed among some individuals, although not to the point of obvious morbidity. Accordingly, this experimental treatment was extended for an additional 30 days (Group C_1) to allow sufficient time for these eels to regain condition. The average weight of eels at the beginning of the second phase of this experiment was 7.81 ± 1.9 g. After an additional 30 days the mortality rate of the eels increased and varied substantially among tanks (15.0 ± 20.1%) yet with a weight gain per surviving eel of 0.6 ± 1.1 g (7.6 ± 12.5% of initial body weight; SGR 0.2 ± 0.4). All mortalities in Group C_1 occurred within the first 11 days of the second phase, with none thereafter. The total mortality rate after the first and second phases of the experiment was estimated to be 16%, similar to the mortality rate observed for Group B.

4 | DISCUSSION

Results of this study are consistent with field studies that showed survival rates to be worse among farmed eels released into the wild when compared to wild eels and stocked glass eels (Pedersen, 2000; Pedersen & Rasmussen, 2016; Simon & Dörner, 2014; Wickström, 2001). This also calls into question current recommendations for stocking glass and on-grown eels into Lithuanian water bodies at a ratio 4:1. After 30 days of feeding on *Chironomus* spp. under laboratory conditions there were no significant differences in survival rates between groups A and C, but the survival rate of Group B was significantly lower. The negative SGR in Group C after the initial 30-day period was due to weight loss and apparent poor physical condition among some individuals. Positive SGR values for groups A and B indicated that these eels were able to gain weight on the *Chironomus* spp. diet. Chironomids have been reported to be one of the main food items among eel stomach contents, even when the aquatic environment had only low abundance of larvae (de Nie, 1982). The survival rate for the eels in the Group C_1 treatment decreased by an additional 15%, but the SGR in the survivors increased to become positive. It is plausible that if Group B had also been extended for a further 30 days as the Group B_1 and no further mortalities had occurred, then there would have been no difference between the two on-grown treatments and both would have differed significantly from Group A, thereby further strengthening support for an hypothesis of superior performance of glass eels.

Kearney, Jeffs, and Lee (2011) suggested a link between initial energy reserves in the shortfin glass eel (*Anguilla australis*) and its survival in captivity. This might explain the observations in our study where larger eels that were well-nourished in the aquaculture facility had accumulated enough energy reserves to cope with an impaired ability to adapt to feeding on *Chironomus* spp. or had an insufficient food intake during the first 30 days, thereby delaying the onset of mortality as observed during the beginning of the second 30-day phase of the experiment. Such phenomena might be related to a sudden change in food from dry formulated fed to a naturally occurring live prey. This is a hypothesis also supported by Bohlin, Sundström, Johnsson, Höjesjö, and Pettersson (2002) and Sundström, Bohlin, and Johnsson (2004), who suggested that decline in condition and growth among brown trout (*Salmo trutta*) was often observed after sudden transition from formulated to wild food. The decrease in the Group C_1 survival rate of 15.2%, compared to only 1% during the first 30-day interval of Group C, we attribute to insufficient food intake. These losses may have contributed to the increase in the final average SGR during the second phase with the elimination of weaker eels from the group.

Although this experimental study was conducted in a laboratory that cannot emulate the environmental conditions encountered by eels following their release into natural water bodies, the overall results imply that the ability of eels to wean from formulated food to natural prey is to some extent limited by the duration of time spent consuming a formulated diet. We acknowledge that the 30-day experimental period may have been less than optimal for testing, and that growth rates on specially formulated feed under farm conditions were better than what was achieved with *Chironomus* spp. larvae during this study. Our study suggests that although on-growing with formulated food provides reserves against starvation, this cannot fully compensate for reduced capability to adapt to feeding on wild prey. This inference is supported by Smirnov et al. (1994), who concluded that hatchery-reared fish used for stocking might be unable to adapt to natural food consumed by wild fish and as a result, stocked fish are often considered to be inefficient feeders unable to adapt to the consumption of natural prey (Maynard, McDowell, Tezak, & Flagg, 1996; Olla, Davis, & Ryer, 1998; Paszkowski & Olla, 1985). As a result, released fish can show substantial weight loss (Baer, 2009). This suggests that fish fed with formulated food might in some cases suffer from post-release starvation caused by impaired ability to locate or correctly identify food items in the wild.

Simon, Dörner, Scott, Schreckenbach, and Knösche (2013) showed that eels released into the wild at the glass eel stage exhibited a superior performance after 4 years than those sourced from commercial farms where they had been on-grown to a larger size. Simon et al. (2013) concluded that eels stocked as farm eels require more time to adapt to natural prey and to develop new foraging strategies than eels stocked as glass eels, whereby during this adaptation period the eels rely on stored energy reserves.

Survival rates in the wild are likely to be lower than those in this study. Hatchery-reared fish are known to show poorly developed predator-avoidance behaviour (Einum & Fleming, 2001; Olla et al., 1998; Youngson & Verspoor, 1998). Larger eels may suffer less predation in the wild due to their size, but if time spent in farm tanks affected their ability to evade or escape predators, then their survival rates would likely be lower. In any event, poorer survival among larger eels retained in captivity for longer will translate into reduced cost effectiveness.

Group A, exposed to aquaculture conditions for a relatively short time, exhibited superior ability to switch from cod roe to *Chironomus* sp. larvae compared to those on-grown on formulated feed for periods of 42 days or longer. Despite implications from this study, the use of on-grown eels for stocking might be unavoidable because glass eels are often available only at the end or beginning of the year, when the surface waters of most lakes in Northern Europe are frozen. ICES (2013) recommends stocking on-grown eels as a better option than glass eels in situations where water temperatures are very low, which may lead to only modest glass eel survival. Considering the results of the current study and similar findings in field studies, it could be argued that eels should be stocked as soon as possible after capture, or at least kept under aquaculture farm conditions for the shortest duration feasible, and, when possible, fed—or at least weaned—with natural food prior to release to improve their ability to adapt to the natural conditions found in the wild. The lack of superior survival rates among on-grown eels also suggests that a policy of releasing glass eels at a four-fold greater rate than on-grown eels on the basis of weight equivalency and presumed poorer survival may be ill founded. If future studies of glass and on-grown eel survival in the wild display similar survival patterns to what we observed in the laboratory, then a revision of recommendations for stocking densities should be considered.

5 | CONCLUSION

Results of the current study suggest that on-grown eels had no survival advantage in comparison to glass eels when fed *Chironomus* spp. in the laboratory, likely because eels must switch their diet from formulated to natural food, a transition with which at least some on-grown eels appear unable to cope.

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II.

Mortality of Silver Eels, *Anguilla anguilla* (Linnaeus, 1758), Migrating Through Different Types of Hydropower Turbines in Lithuania

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Abstract

Hydropower plants (HPP) are considered to be one of the major threats to the survival of European eels when migrating downstream along inland waterbodies during the early part of their annual journey to the spawning area in the Sargasso Sea. There are 98 HPPs in Lithuania and thousands throughout Europe. Numerous studies describe mortality rates among European eels caused by HPPs as variable depending on various local, environmental and technical factors. This heterogeneity in effect complicates theoretical extrapolation to eel mortality arising from different HPPs, necessary for effective management of local stocks. Silver eel mortality was estimated for four different HPPs in Lithuania. Mortality was estimated using RFID (PIT) tags and acoustic telemetry in a large HPP (>100 MW) with Kaplan turbines, a small HPP (<1 MW) with a Kaplan turbine and fish ladder, and for the first time in two small HPPs (<1 MW) with CINK turbines. The results supported a hypothesis that the mortality rate of migrating eels depends mainly on the type and size of the turbine. HPP induced mortality varied from 100% in a small CINK turbine down to 23.8% in the large HPP with Kaplan turbines. The importance of simple mitigation measures was highlighted by 34% of all tagged eels bypassing the HPP via a fish ladder constructed for upstream migration of salmonids. The observed differences in mortality provide essential information for long term strategies designed to restore depleted eel populations in Lithuania and other European countries.

Key words: *Anguilla anguilla*, hydropower, eel migration, Kaplan turbine, CINK turbine

Introduction

Steep declines in European eel *Anguilla anguilla* recruitment started in the 1980s and since then eel population abundance has fallen outside safe biological limits (Dekker, 2004; ICES, 2006). This population crash happened over the entire range of this species' distribution without a single obvious cause, but a number of different reasons such as changes in the Gulf stream, migration barriers, fishing pressure, habitat loss, parasites or pollution have been postulated (Dekker, 2004; Wirth, 2003). Despite all these factors contributing to the decline in eel populations there is no consensus on their relative importance. Results from previous studies (e.g. Winter et al., 2006; Bruijs and Durif, 2009; Aarestrup et al., 2010) demonstrated that substantial mortality during downstream migration of eels, which in Lithuania is most intensive in spring (Ložys et al., 2008), could dramatically reduce the number of spawners. Fisheries and loss from passage of hydropower plants (HPPs) are often considered to be the main causes of eel mortality in rivers (Winter et al., 2006). The two principal direct causes of mortality at HPPs are turbine-related trauma and impingement on protective screens (Monten, 1985; Calles et al., 2010).

It has been generally assumed that turbine related mortality of migrating fish decrease with increasing turbine size (Calles et al., 2010). However, eel mortality rates in HPPs are variable depending on the site, river physiography, associated hydrological conditions, and the type of migration barriers installed (ICES, 2007). Eels tend to have 4 to 5 times higher mortality rates compared to e.g. juvenile salmonids when transiting HPPs (Hadderingh and Baker, 1998), mostly due to mechanically-induced injuries because of their elongated morphology (Monten, 1985; Larinier and Travade, 2002). Previous studies have demonstrated negative impacts of hydropower on migrating eels, with mortalities ranging from 5 to 100%. Kaplan turbines are the most commonly used in Europe (Bruijs and Durif, 2009) and according to Larinier and Travade (2002) the range of reported mortality is between 15% and 30% in large Kaplan turbines, and from 50% to 100% in the smaller turbines used in most small-scale HPPs (Monten, 1985; Hadderingh and Baker, 1998). We did not find any studies on the rates of eel mortality in cross-flow turbines (e.g. Banki, CINK, Ossberger), however, mortality rate of other fish species passing through cross-flow turbines is significantly higher (up to 75%; Gloss and Wahl, 1983; DuBois and Gloss, 1993) compared to that in Kaplan or Francis turbines. Many behavioural studies (e.g. Calles et al. 2010; Behrmann-Godel and Eckmann 2003; Durif et al., 2003) suggest that eels approaching HPPs and dams often hesitate to continue with their migration, thereby extending their migration time. Pedersen et al. (2012) reported that some of eels spent weeks moving in and out of the power canal before finally passing or disappearing beyond the detection range. In that study only 23% of the tagged eels reached the tidal limit within the study period, mainly due to difficulties in traversing the hydropower dam.

Global production of hydroelectricity has grown steadily by about 3% per year on average since 1980 (Moller, 2016). The role of hydropower, along with other renewable energy sources, is expected to become increasingly important in the future. The highest growth rates are expected in developing countries with high but unexploited hydropower potential, e.g. parts of Eastern Europe (Voigtländer et al., 1999). Thus, the negative impact of HPPs on migrating fish is likely to increase in the future.

The main objective of this study was to assess mortality rates of silver eels passing low-head HPP turbines of two types: Kaplan (large and small) and CINK (small). An additional aim of the study was to estimate the importance of fish ladders for bypassing HPP during downstream eel migration.

Study area

The study area encompassed part of the Nemunas River catchment and several of its tributaries in which a total of eight HPP are located four of which were included in this study (Fig. 1). The Nemunas River is the largest river in Lithuania, with a total length of 937 km and catchment area of 98 200 km^2. The Kaunas HPP with four Kaplan turbines was built on Nemunas River in 1960 and is situated 223 km upstream the Curonian lagoon with a further 67 km to the Baltic Sea (Table 1). The dam creates the 63.5 km^2 Kaunas water reservoir above the HPP. There are no other fish migration barriers between the Kaunas HPP and the Baltic Sea.

Figure 1. Location of Pabradė, Bagdononys, Valtūnai and Kaunas HPPs, and others within the catchments that were not included in this study.

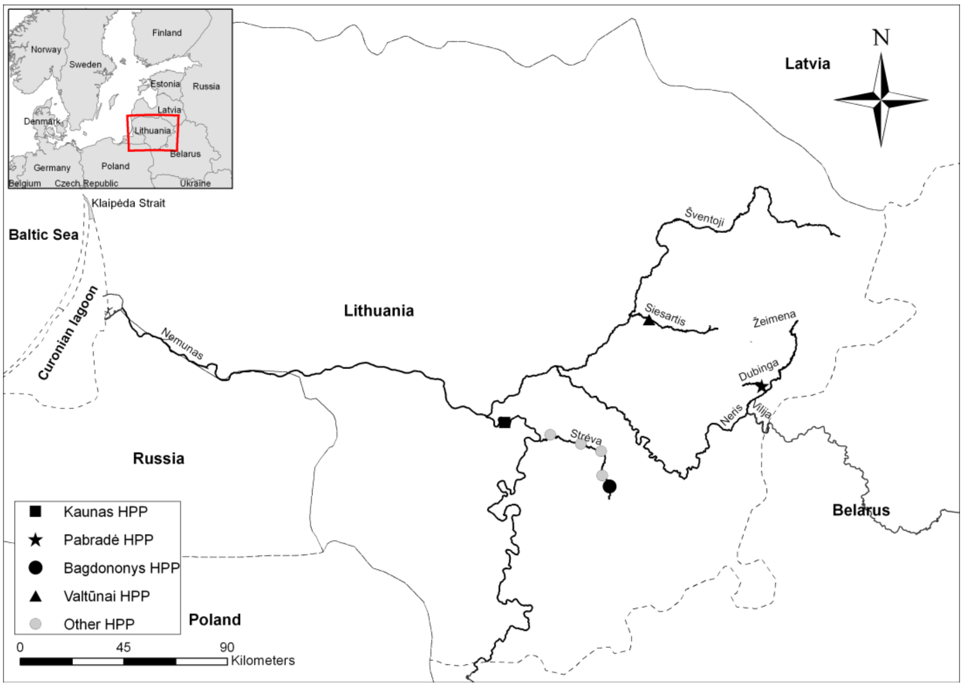

Table 1. Main technical parameters of studied HPPs (Lithuanian hydropower assotiation, 2011).

River	HPP	Turbine	Water head, m	Installed power	Mean annual river flow at HPP, $m^3 s^{-1}$
Nemunas	Kaunas HPP	Kaplan	15	101 MW	375
Siesartis	Valtūnai HPP	Kaplan	3.8	170 kW	5
Strėva	Bagdononys HPP	CINK	10.9	90 kW	0.8
Dubinga	Pabradė HPP	CINK	10.5	315 kW	3.4

The Siesartis River (Fig. 1) is 64 km long and its catchment area is 616 km^2. This river is dammed by Valtūnai HPP at 11 km from its confluence (377 km from the Baltic Sea) (Table 1); there are no other fish migration barriers between the HPP and the Baltic Sea.

The Strėva River is 74 km long and its catchment area is 759 km^2; the river drains to the Kaunas water reservoir above Kaunas HPP. The Bagdononys HPP with one cross-flow CINK turbine is situated 60.5 km from the mouth of Strėva River and 412 km from the Baltic Sea (Table 1, Fig. 1). The Strėva River is dammed by five HPPs at 9, 30.4, 40.5, 56.6, and 60.5 km from the river's mouth.

The Dubinga River is 17.8 km long and its catchment area is 410.4 km^2. The Pabradė HPP (Table 1) is located 1.4 km from the mouth of Dubinga River and 540 km from the Baltic Sea (Fig. 1) with no other fish migration barriers between the HPP and the Baltic Sea.

Materials and Methods

Large Kaplan turbine

To assess mortality rates of eels migrating downstream through large Kaplan turbines installed at the Kaunas HPP, 25 silver eels were caught in a small tributary of the Nemunas River upstream of the HPP. Immediately after capture the eels were translocated to the release site (~60 km) near Kaunas HPP in plastic transportation bags supplied with water and oxygen. Then the eels were placed in submerged cages to allow full recovery after transportation prior to surgery. Eels were anaesthetised with 2-phenoxy ethanol (0.8 ml l^{-1}) for 5–10 minutes. A ~12–15 mm incision for Vemco V9 tags (weight 4.7 gram in air, length 29 mm, estimated tag life 159 days) and ~18–22 mm incision for Vemco V13 tags (weight 11 gram in air, length 36 mm, estimated tag life 262 days) was made on the mid-ventral line, in the posterior quarter of the body cavity. V9 tags were used to tag eels between 352 and 550 g while V13 tags were used for tagging eels >550 g. Tag-to-body weight ratios varied between 0.6 and 1.9%. The transmitter was inserted into the intra-peritoneal cavity and positioned 3–4 cm anterior of the incision. Surgery took 5–6 minutes to complete and the incision was then sutured with 4/0 Vicryl®Polyglactin absorbable surgical thread and treated with antiseptic *Methylrosanilinni chloridum* 2% solution. After the surgery eels were transferred back to the cages for recovery from anaesthesia for 20-30 minutes. The V13 tags in the larger eels were selected for the longer battery life necessary to track silver eels over a long period, but these migration data are not presented as they were beyond the scope of the current study. Despite its relatively big size the V13 tag has been previously used to successfully tag silver eels (Westerberg et al. 2007, Béguer-Pon et al. 2014) without causing increases in mortality rates (Winter et al., 2005; Heupel et al., 2007). After recovery, the tagged eels were released into the reservoir near the Kaunas HPP intake (N=13 on May 30, N=3 on June 13 and N=9 on October 7, 2014) between 10 a.m. and 12 a.m.

The eel silvering stage was determined as described by Durif et al. (2009). Fulton's condition factor (FCF) was calculated as described by Ricker (1975). All silver eels >55 cm were considered to be females (Tesch, 1977).

Four receivers were installed in the area of Kaunas HPP water intake to detect eels entering turbines; four receivers were installed just below the Kaunas HPP to detect eels that had passed through the turbines. Data from the receivers was downloaded monthly. Time taken to pass through the turbines was calculated as the time-lag between the last detection of an eel upstream of the HPP and the first detection below the HPP. To detect eels that successfully migrated downstream, four additional receivers were installed on the navigational buoys within the Nemunas Delta.

To locate eels that had passed through the Kaunas HPP but had become possibly lethally injured, a section of the Nemunas River 25 km below the HPP was scanned with two VR2W receivers installed on an inflatable boat prior to the end of transmitter's estimated battery life.

Small CINK and Kaplan turbines

Eel mortality in the small CINK (Bagdononys HPP and Pabradė HPP) and Kaplan turbines (Valtūnai HPP) was assessed from eels tagged with 12 mm passive integrated transponders (PIT tags). Eels migrating downstream were captured above each HPP using a fyke net. Immediately after capture eels were anaesthetised as described above and fitted with PIT tags injected into the peritoneal cavity. After recovery the tagged eels were translocated approximately 2 km to Bagdononys and about 2.5 km to Pabradė HPPs. After transportation the eels were allowed to recover for c. 30 minutes and using the guidance system described by Oliveira and Pressiat (2011) they were released as close as possible to the turbine's water intake pipe. This release strategy aimed to avoid losses of tagged eels above the HPP due to caseation of migration or predation. Following their passage through the turbine eels were recaptured below the HPP in a fyke net.

The Valtūnai HPP does not have a water reservoir above the dam wall, thus tagged eels were released just below the site of capture - approximately 800 meters from the HPP. After release, the eels migrated downstream and were recaptured below the HPP or in a fish ladder. Fyke nets set below and above the HPP were checked every 30 minutes to remove trapped eels and were only removed from the river after all of the PIT tagged eels had been recaptured.

Immediately after recapture eels were euthanized by an overdose of anaesthetic. After euthanasia eels were scanned for their ID numberand transported to the Lithuanian Nature Research Centre for further analyses. Injuries were considered to be lethal if an eel's spine or skull were fractured or if the internal organs had evidence of severe trauma. Other fish species, if any, caught below HPP were also examined for injuries.

Morphometric parameters (TL; W), FCF and the silvering stage of eels used for evaluation of mortality rates in CINK and Kaplan turbines are presented in Table 2.

Table 2. Morphometric parameters and tagging method of eels used for evaluation of mortality rates caused by CINK and Kaplan turbines

HPP	**Turbine**	**N**	**Tagging method**	**TL, mm (±SD)**	**W, g (±SD)**	**FCF (±SD)**	**Silvering stage**
Bagdononys HPP	CINK	52	PIT	681±84	576±153	0.18±0.04	FIII (N=20) FV (N=32)
Pabradė HPP	CINK	26	PIT	691±51.9	629±139	0.19±0.04	FIII (N=6) FIV (N=1) FV (N=19)
Valtūnai HPP	Kaplan	64	PIT	681±73	545±174	0.17±0.02	FV (N=64)
Kaunas HPP	Kaplan	25	Acoustic VEMCO	761±93	897±398	0.19±0.03	FIV (N=7) FV (N=18)

Eel mortality rate was calculated as the ratio between the number of tagged eels that passed through the turbines and the number of eels which survived without suffering lethal injury.

As the data for eel length, weight and FCF was non-normally distributed (Shapiro–Wilk's W tests, $p<0.05$), the non-parametric Mann-Whitney test was used to test for the effect of length on eel survival during passage through the turbine, and choice of migration route through turbine or fish ladder, as well as the effects of length and weight on migration success from Kaunas HPP to the Nemunas Delta.

Results

Small CINK turbines

All 52 eels released upstream from Bagdononys HPP passed the turbine immediately after release and were recaptured below the HPP. All eels suffered lethal injuries causing 100% mortality. All other fish caught below Bagdononys HPP experienced 100% mortality. These included Roach (*Rutilus rutilus*)

N=12, mean TL 8.8±1.1 cm; Tench (*Tinca tinca*) N=1, TL 7.5 cm; and Bleak (*Alburnus alburnus*) N=6, mean TL 11.3±0.2 cm.

Laboratory examination revealed that all eels suffered fractures of the spine and injuries to their internal organs; most eels (N=44, 84.6%) suffered laceration of skin and muscles. Thirty four eels (65.4%) had fractures of the skull. Marks from the turbine runner were evident over the entire body surface. The mean number of spinal fractures was 12±2 per eel.

Out of 26 eels guided to the Pabradė HPP water intake pipe none were recaptured below the HPP.

Large Kaplan turbine

There is no fish ladder installed on the Kaunas HPP and its spillway operates only during extreme flooding events ensuring that all migrating eels had to pass directly through the turbines. Out of 25 eels released upstream of the Kaunas HPP water intake area, 21 (84%) moved downstream through the turbines and were detected below the HPP. Twelve eels migrated within 24 hours after release, while nine eels delayed passing through by one to 47 days. Three of them stayed close to the HPP water intake zone prior passing through the turbines, whereas remaining six eels were moving actively in and out of the water intake area prior to passage. Four eels did not migrate downstream and remained in water reservoir until the end of transmitter battery lifespan. A majority of eels (76%, N= 16) migrated through the HPP during daylight hours between 9.00 a.m. and 8.00 p.m., whereas another 5 eels (24%) migrated during night time between 10.00 p.m. and 5.00 a.m. The mean TL among eels which failed to migrate and instead stayed within the Kaunas Reservoir was 690±71 mm, and mean W is 534±65 g, whereas eels detected below the Kaunas HPP were 775±93 mm in length with the mean 967±398 g weight. There were no statistically significant differences ($p>0.05$) in TL and FCF between of these two eel groups, whereas eels that did not migrate through turbines had significantly lower W ($p<0.05$). Time taken to pass the Kaplan turbines was diverse and varied between 35 seconds and almost ten hours, but more than half of all eels (N=12, 57%) passed through the turbines within 5 minutes. Statistical analysis demonstrated that there was no significant difference between time taken to pass the turbines when comparing eels which reached the Nemunas Delta and those which have not.

Out of 21 eels which migrated through turbines, 11 (52.4%) were detected in the Nemunas Delta (212 km downstream from Kaunas HPP). Transmitters showed that five eels (23.8%) remained stationary in close proximity to the Kaunas HPP (from 0.5 km to 6.2 km) until the battery was discharged. As a consequence it was concluded that these eels had died. The fate of the remaining five eels after passing through the HPP turbines remains unknown because the transmission signal ceased between the scanned sector of 25 km downstream HPP and the Nemunas delta.

Eels that successfully reached the Nemunas Delta were slightly smaller (mean TL=762±84 mm and W=874±281 g), compared with eels that migrated through turbines but did not reach the Nemunas Delta before the transmitter battery expired (mean TL=790±104 mm and W=1070±491 g). This difference was not significant and neither was the difference in W between the two groups. Four (36.4%) out of 11 eels detected in the Nemunas Delta were at the silvering stage FIV, while the other seven eels (63.4%) were at the silvering stage FV. Four (80%) out of five eels that suffered lethal injuries during passage through the Kaplan turbines were at the silvering stage FV and one (20%) at silvering stage FIV. Three (60%) out of five eels that disappeared between the scanned sector downstream of the Kaunas HPP and the Nemunas Delta were at the silvering stage FV and two (40%) at the silvering stage FIV.

Small Kaplan turbine

Following release, all tagged eels (N=64) passed the Valtūnai HPP during the same night. The most intense passage was observed between 0.30 a.m. and 4.30 a.m. when 83% (N=53) of the eels were recaptured below either the HPP or the fish ladder. All recaptured eels had implanted PIT tags and no other eels were caught. Forty two eels (66%) migrated through the turbine, while the remaining 22 eels (34%) were caught after passing through the fish ladder. Eels caught passing through the fish ladder were significantly larger (p<0.001, mean TL=72.0±7.2 cm, W=681±188 g) than eels passing directly through the turbine (mean TL=66.1±6.4 cm, W=476±109 g); their FCF was also significantly larger (p<0.001, mean FCF=0.18±0.02) when compared with eels passing directly through the turbine (mean FCF=0.16±0.02). Eel mortality in the Kaplan turbine at Valtūnai HPP was estimated to be 52.4% because 22 out of 42 eels suffered lethal injuries while passing through the turbine. During same period, out of 29 salmonid juveniles (TL=12.8±1.2 cm) that were caught below the Valtūnai HPP, eight (27.6%) suffered lethal injuries during their turbine passage, while the rest were without any visible injuries.

Laboratory examination indicated that 20 (48%) out of 42 eels that migrated through the turbine suffered fractures of the spine, 14 eels (33%) suffered injuries to their internal organs, and 18 eels (43%) had lacerations of their skin and muscles. Two eels (5%) had skull fractures. Marks from the turbine’s runner (absence of scales or small scratches) were visible on 38 out of 42 eels (90.6%), but in only 22 cases (52%) were these injuries lethal.

There were no significant differences (p>0.05) in mean length, weight and FCF between eels that suffered lethal injuries (N=22; TL=67.3±7.6 cm, W=494±131 g, FCF=0.16±0.02) and those which passed through the turbine successfully (N=20; TL=64.8±4.5 cm, W=458±77, FCF=0.17±0.01).

Discussion

Results of this study support conclusions from similar studies (e.g. Hadderingh and Baker, 1998; Verbiest et al., 2012) that show the occurrence of substantial mortality among silver eels due to injury when passing through HPP. It is apparent that HPP are among the main factors liable for decline in eel stocks.

Successful eel migration through small cross-flow CINK turbines was virtually impossible with 100% mortality recorded at the Bagdononys HPP. This HPP does not have a fish ladder, thus all eels passed through the turbine suffering lethal injuries as a consequence. We conclude that cross-flow CINK turbines should be considered as the most hazardous type for migrating eels. Mortality rates of juveniles of other fish species (e.g. shad and salmonids) in cross-flow turbines has been reported to be up to 75% (Gloss and Wahl, 1983; DuBois and Gloss, 1993), but in the current study the mortality among other fish species (roach, bleak, tench) in the small cross-flow CINK turbine was estimated to be 100%.

None of 26 eels guided into the Pabradė HPP water intake pipe were recaptured below the HPP. After the field experiment was conducted, it was found out that the HPP was equipped with an additional protective screen in the water intake pipe with a bar interval of c. 10 mm. This protective screen was not included in the initial HPP construction design and could not be reasonably known in advance of this study. It presence was only discovered after the field experiment during attempts to identify reason for the ‘disappearance’ of all tagged eels guided into intake of the turbine. This implies that effective screening in the absence of fish ladder or other effective way for eels to bypass turbines will cause cessation of eel migration, as eels either would be impinged in the screen or unable to find a way to continue their migration. On the other hand, the experiment demonstrated effectiveness of 10 mm bar intervals in preventing eels of being drawn into turbines and suggests that screening materials of similar dimensions could be used for the constructions of bypasses to guide migrating eels away from the intakes of turbines and redirect them towards fish ladders.

Eel mortality rates in HPPs can be significantly reduced by fish ladders. A substantial proportion of eels (34%) at Valtūnai HPP migrated through the fish ladder thereby avoiding the injuries suffered by those which had passed through the Kaplan turbine. Our findings contrast with studies reporting only sporadic usage of ladders (originally designed for fish upstream migration) by eels migrating downstream (Verbiest et al., 2012; Jansen et al., 2007). Eels caught during passage via a fish ladder were significantly larger and had higher FCF in comparison with those passing directly through a turbine. This is presumably caused by protective 35 mm metallic screens at the HPP water intake zone which prevent larger eels from entering the turbine. Fish with elongated morphology tend to have higher mortality rates compared with other morphologies (e.g. salmonids) (Monten, 1985; Larinier and Travade, 2002), implying that larger eels were also expected to suffer higher mortality rates. However, there were no significant length and FCF differences between eels which suffered lethal injuries during passage through the small Kaplan turbine and those that survived. Length variation among eels which passed through the turbine was relatively small (from 57.5 to 85 cm) in our study, hence small males that usually grow up to 35 cm (Bauchot, 1986) are likely to have lower mortality rates.

According to national regulatory measures to protect fish from small hydropower plants, each small HPP in Lithuania must have turbine screening by metal grids with bar intervals <35mm, but in practice the grids are not less than 35 mm. Our results indicate that such screening is insufficient for protection of eels and approximately two thirds of eels at the Valtūnai HPP pass directly through the turbines. ICES (2007) recommends that small male silver eels require bar intervals <9mm for protection, whereas females may be prevented from entering turbines by bar intervals <15mm. Different screens and trash racks in front of water intakes have also been known to cause damage if fish are impinged and pressed against the racks by strong water currents (Adam and Bruijs, 2006; Calles et al., 2010), however the average flow rates of Lithuanian lowland rivers are relatively slow and in conjunction with large bar intervals of ~35mm, impingement on screens should be negligible, if any. Installation of effective screens at HPP in combination with fish ladders may reduce eel mortality rates to negligible levels. However, in Lithuania only three new fish ladders were installed during past nine years which is evidently insufficient to significantly reduce eel mortality rates. If such improvements were undertaken then more water bodies may become suitable for restocking and restoration of depleted eel populations.

The majority of the 98 HPPs built on Lithuanian rivers (N=67, 68%) use Kaplan turbines, as with the rest of the Europe (Bruijs and Durif, 2009). According to the Bruijs and Durif (2009) review, eel mortality in Kaplan turbines at large (>10 MW) HPPs typically ranges from 20% to 38%, thus the results of the current study fall within an expected mortality range. Out of 21 eel which have passed Kaplan turbines in the Kaunas HPP, 5 eels (23.8%) remained stationary below HPP until the transmitter’s battery expired, suggesting that the chance that they were still alive was negligible. The fate of the other 5 eels, which disappeared somewhere between the scanned sector 25 km downstream of the HPP and the Nemunas Delta remains unknown. Winter et al. (2006) and Aarestrup et al. (2010) suggest that some migrating eels cease migration for lengthy periods, thus it is likely that those eels survived. Tag induced morbidity and mortality are also considerations when tracking migrating eels. Jepsen et al. (2002) suggests that tag size should be minimized as much as possible. Cottrill et al. 2006 demonstrated that swimming capacity of silver American eels is not affected by the presence of telemetry transmitters and surgically implanting transmitters is the preferred method of affixing telemetry transmitters, especially for long-term telemetry studies. Despite the V13 acoustic tags being relatively large, we assume that they had no significant negative impact on eel swimming performance and behaviour as it was suggested by Westerberg et al. (2007) and some most recent studies (e.g. Besson et al. 2016) have tagged eels with a higher tag to body mass ratio (>2.5%).

Considerably higher mortality rate for eels passing through the Kaplan turbines installed in the Valtūnai HPP was likely caused by the smaller size of the turbine, given that turbine related mortality is expected to be decreasing with increasing size of turbine (Marmulla, 2007).

Despite eels being typically nocturnal animals (Tesch, 1977) more than half of the eels passed through the Kaunas HPP turbines during daytime. Durif (2003) suggests that eel migration during daytime is related to increased water turbidity and water flow rate. The mean depth of the Kaunas Reservoir is approximately 12 m and water turbidity is relatively high, therefore eels were exposed to a relatively dark environment even under conditions of daylight during passage through the turbines, which are located near the bottom (in ~15 m depth). This daytime behaviour was observed only in the Kaunas HPP. In the small rivers with shallow depth (Siesartis, Dubinga and Strėva) eels were captured only during night time. Previous behavioural studies (Behrmann-Godel and Eckmann, 2003; Durif et al., 2003; Gosset et al., 2005; Calles et al., 2010) suggested that HPPs and dams may have indirect negative effect on eel migration: migrating eels often delay their passage through an obstacle and consequently their migration becomes extended. Results of the current study support this observation as 36% of eels released upstream from the Kaunas HPP also delayed passing through the turbines for periods from one to 47 days, while 16% of eels did not migrate at all. The remaining 48% of tagged eels passed turbines of Kaunas HPP within 24 hours after their release.

We conclude that all eels passing through small CINK turbines suffer lethal injuries resulting in 100% mortality, whereas Kaplan turbines cause lower mortality rates ranging from c. 24% to 52% depending upon size of the turbine. Results from this study suggest that 34% of eels migrating downstream used fish ladders, originally designed for upstream migration of salmonids. Installation of fish ladders, especially in combination with effective screening, may be an effective measure to substantially reduce mortality rates among migrating eels. The results of our study demonstrate that HPPs may significantly threaten escapement targets specified in eel management plans if re-stocking is conducted in water bodies upstream from HPPs in the absence of any mitigation.

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ORIGINAL ARTICLE

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Silver eel, *Anguilla anguilla* (Linnaeus, 1758), migration patterns in lowland rivers and lagoons in the North-Eastern region of their distribution range

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Summary

Escapement success and migration patterns of silver eels *Anguilla anguilla* (L.) was studied by acoustic telemetry in three natural free-flowing and one dammed river and in Curonian Lagoon in Lithuania. Mean downstream migration speed and escapement success were almost the same in the shorter 210 km dammed river (52%, 13.6 km/day) and the considerably longer 300–480 km free-flowing rivers (53%, 10.7 km/day). Despite the similarity between migration speed in the Curonian Lagoon (14.6 km/day) to that in rivers, migration success was significantly higher (71%) in the Lagoon. Although a majority of silver eels in Lithuania start migrating downstream in spring, the peak of eel migration into the Baltic Sea was observed during late fall. Overall migration success in the rivers and the Lagoon was 35%. Relatively low escapement may have negative consequences on the success on eel stock restoration and must be addressed when strategically planning for the production of spawners.

1 | INTRODUCTION

Since the 1970s, recruitment of the European eel (*Anguilla anguilla* L.) has declined over 90% due to various causes, such as migration barriers, habitat destruction and pollution, fisheries, diseases and parasites (Dekker & Casselman, 2014). Previous studies (Aarestrup et al., 2010; Bruijs & Durif, 2009; Winter, Jansen, & Bruijs, 2006) demonstrated that substantial mortality during downstream migration could dramatically reduce the number of silver eels. The main causes of this mortality are fishing and lethal injuries from passage through the turbines of hydropower plants (HPP) (Winter et al., 2006).

The practice of stocking eels in Lithuania has endured for decades, but eels were originally released to bolster commercial or recreational fisheries without aiming to facilitate migration to increase spawning. Eels were often stocked above HPP or dams thereby incurring substantial mortalities (Winter et al., 2006) and disruption of migration (Legault, Acou, Guillouet, & Feunteun, 2003). Despite the 98 HPPs and 1,025 dams constructed in Lithuania, the main eel migration routes to the Baltic Sea are along free flowing rivers or river sections of up to c. 600 km (Ložys, Repečka, Pūtys, & Gurjanovaitė, 2008). Despite numerous studies about eel mortality arising from passage through HPPs, there are scant data available on eel escapement success or downstream migration speed within free flowing rivers (e.g., Bultel et al., 2014; Simon, Berends, Dörner, Jepsen, & Fladung, 2011; Stein et al., 2016) and lagoons (e.g., Amilhat, Farrugio, Lecomte-Finiger, Simon, & Sasal, 2008; Charrier et al., 2012). Lithuania's free flowing lowland rivers differ in terms of hydrological conditions (40% of discharge comes from melted snow, 35% from ground water and only 25% from rain), temperature (2–3 months per year rivers are covered with ice); degree of regulation (most large rivers are natural and historically were not regulated); and flow regime (in spring due to melting snow discharge, flows are 2–3 times higher than in other seasons) compared to Western Europe (Gailiušis, Jablonskis, & Kovalenkovienė, 2001). In the context of concerted international efforts to restore eel stocks, it is therefore also important to determine the main patterns of silver eel migration in the rivers of North Eastern Europe.

The objective of this study was to assess overall escapement success and migration patterns of silver eels migrating through natural free-flowing and dammed rivers in Lithuania, prior to escaping to the Baltic Sea via the Curonian Lagoon.

2 | MATERIALS AND METHODS

2.1 | Study area

Eel migration was studied in four rivers: the Neris, Siesartis and Žeimena in which they could migrate freely downstream, and the Nemunas in which eels had to pass through a HPP.

The Kaunas HPP with its four low head Kaplan turbines is built on Nemunas River (Figure 1), c. 223 km from the Curonian Lagoon and c. 290 km from Baltic Sea. The height of the dam is 24.6 m, water head 15 m, installed power 100.8 MW with maximum flow of 760 m^3/s (Lithuanian Hydropower Association, 2011). The dam creates the 63.5 km^2 Kaunas Water Reservoir. There are no other migration barriers or regulating structures which impede river flow between the Kaunas HPP and the Baltic Sea.

The Neris River (Figure 1) is a tributary of the Nemunas River, and besides the Vileika HPP upstream in Belarus, there are no other migration barriers or other flow regulating structures on the river in Lithuanian territory.

The Siesartis River is dammed by one HPP with a pool and weir type fish ladder installed 11 km upstream from the river mouth, but eels were released below this HPP. The Žeimena River (Figure 1) is free-flowing throughout its entire length. The main morphological and hydrological parameters for each of these rivers are presented in Table 1.

The non-tidal Curonian Lagoon is a shallow semi-enclosed water body covering 1,584 km^2 adjacent to the South Eastern rim of the Baltic Sea (Figure 1). The southern and central regions of the Lagoon are freshwater while the northern part is oligohaline with irregular salinity fluctuations up to 8 ppt (Zettler & Daunys, 2007). The Nemunas River provides the main water inflow into the Lagoon, which discharges to the Sea through Klaipėda Strait.

2.2 | Eel tagging

A total of 63 silver eels were caught in four rivers in Eastern Lithuania during their spawning migrations using fyke nets of 16–20 mm mesh size and tagged with Vemco acoustic tags in spring and autumn 2014 (Table 2). Prior to tag implantation, weight, total length, eye diameter, length and height of pectoral fin were measured. The silvering index, based on total body length, body weight, pectoral fin length and mean eye diameter, was determined as described by Durif, van

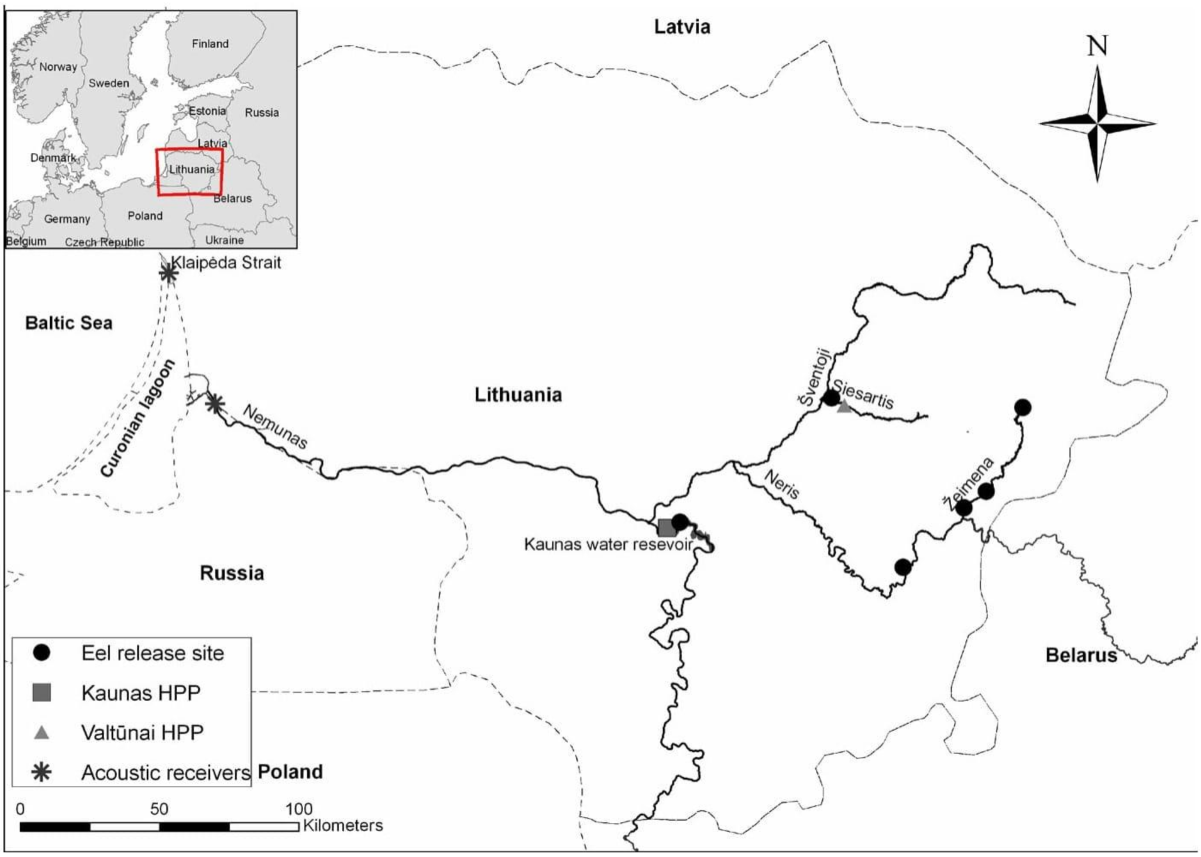

FIGURE 1 Eel release sites in Nemunas, Neris, Žeimena and Siesartis Rivers; the location of Kaunas and Valtūnai HPPs; and the location of acoustic receivers installed in the Nemunas Delta and Klaipėda Strait (four at each location)

TABLE 1 Main parameters of the rivers into which tagged eels were released

				Rain events in the release site		Annual rainfall (mm) in the release site	
River	Length, km	Catchment area, km^2	Mean annual flow, m^3/s	2014	Multiannual average (1981–2010)	2014	Multiannual average (1981–2010)
Nemunas	937	98,200	375	154	180	641	637
Neris	510	25,100	180	166	175	613	685
Žeimena	80	2,793	27	176	175	713	754
Siesartis	64	616	5	158	176	647	659

TABLE 2 Morphological parameters of tagged eels, river slope and the distance of migration route from the release site to the Baltic Sea

Eel catch/ release site	Date	*N*	Length ± *SD*, cm	Weight ± *SD*, g	*K* ± *SD*	Silvering stage	River slope	Distance to the BS, km
Siesartis	20/05/2014	7	76.6 ± 9.4	835 ± 279	0.18 ± 0.01	FIV; FV; MII	0.21	366.9
Žeimena, I	21/05/2014	8	70.9 ± 3.3	636 ± 106	0.18 ± 0.02	FV FV; MII	0.27	549.7
	22/05/2014	2	61 ± 10.0	462 ± 235	0.19 ± 0.008	FV; MII	0.27	549.7
	28/05/2014	8	70.3 ± 8.4	686.9 ± 272	0.19 ± 0.03		0.27	549.7
Žeimena, II	22/05/2014	2	72.0 ± 2.8	696 ± 33	0.19 ± 0.01	FV	0.27	499
Žeimena, III	02/06/2014	7	69.7 ± 5.9	608 ± 200	0.17 ± 0.02	FV	0.25	482.8
Neris	29/05/2014	4	73.2 ± 4.9	719 ± 130	0.18 ± 0.03	FV	0.24	434.4
Nemunas (Kaunas water reservoir)	30/05/2014	13	79.6 ± 8.9	1,045 ± 462	0.2 ± 0.03	FIV; FV	0.1	278
	13/06/2014	3	79.5 ± 4.8	892 ± 167	0.18 ± 0.003	FV FIV; FV	0.1	278
	07/10/2014	9	70.0 ± 8.6	686 ± 248	0.19 ± 0.03		0.1	278

Ginneken, Dufour, Müller, and Elie (2009). All silver eels >55 cm were considered to be females (Tesch, 2003). Prior to surgery eels were anaesthetised with 2-phenoxy ethanol (0.8 ml/L) for 8–10 min. An incision c. 12–15 mm for V9 tags (weight 4.7 g in air, length 29 mm, estimated tag life 159 days, emission delay for first 45 days 20–50 s, later 30–60 s) or c. 18–22 mm for V13 tags (weight 11 g in air, length 36 mm, estimated tag life 262 days, emission delay first 45 days 20–50 s, later 40–100 s) was made on the mid-ventral line, in the posterior quarter of the body cavity. The transmitter was inserted into the intra-peritoneal cavity cranially and positioned 3–4 cm forward of the incision by using a plastic plunger. V9 tags were used to tag eels up to 550 g, while V13 tags were used for tagging eels over 550 g. Transmitter implantation was not expected to affect eel behaviour or cause mortality in this study, as eels were successfully tagged with these transmitters in several other studies (e.g., Simon et al., 2011; Westerberg, Lagenfelt, & Svedäng, 2007). The surgery took 5–6 min to complete. The wound was sutured with 4/0 Vicryl®Polyglactin soluble surgical thread and treated with antiseptic *Methylrosanilinni chloridum* 2% solution. After the surgery eels were transferred to special cages in the site of intended release, where recovery from anaesthesia lasted 30 min (Table 2).

All eels were released in their place of capture (Table 2 and Figure 1) except for those (*N* = 25) released upstream of the Kaunas HPP (eels were caught in a tributary of the Nemunas River c. 60 km upstream HPP).

2.3 | Installation of receivers

Four Vemco VR2W receivers were installed in the vicinity of the Kaunas HPP water intake to detect eels entering turbines and four receivers were installed just below the Kaunas HPP to detect those eels that had passed through. To detect eels that successfully migrated downstream, four receivers were installed on navigational buoys in the Nemunas Delta and four in the Klaipėda Strait (Figure 1).

Range tests were performed at each detection station to ensure complete coverage of the area. All eels that were detected were registered by all receivers deployed along their migration route, hence it is a reasonable assumption that all tagged eels passing within the range of a detection station during the study period would have been recorded.

To locate missing eels, downstream of the eel release sites in the Neris, Žeimena and Siesartis Rivers and a 25 km section of the Nemunas River below the Kaunas HPP were scanned 2 months before the end of the estimated duration of transmitter batteries, with VR2W receivers installed on a boat drifting downstream. In addition, Žeimenys Lake was scanned in case tagged eels had migrated upstream from the Žeimena River.

TABLE 3 Migration success and long term migration speed (V_{long}) of eels in free flowing and dammed rivers and Curonian Lagoon

Release site (River)	N	Detected in the Nemunas Delta, N (%)	Mean V_{long} in rivers ± SD, km/day	Detected in the Klaipėda Strait, N (%)	Mean V_{long} in the Curonian Lagoon ± SD, km/day
Siesartis	7	3 (42.9)	13.1 ± 12.3	2 (28.6)	49.9 ± 23.5
Žeimena	27	13 (48.1)	8.2 ± 5.5	6 (22.2)	10.0 ± 12.8
Neris	4	4 (100)	16.7 ± 20.4	3 (75)	17.5 ± 14.1
Total (free-flowing rivers)	38	20 (52.6)	10.7 ± 10.7	11 (29.0)	19.3 ± 20.4
Nemunas (dammed river)	25 (21)	11 (52.4)	13.6 ± 12.0	10 (40)	9.3 ± 10.7

2.4 | Data analysis

Migration success (MS, %) of the tagged eels was calculated according to the formula:

$$MS = 100 - (100 \times (N_t - N) \div N_t)$$

where: N—number of tagged eels detected by acoustic receivers (in the Nemunas Delta and/or Klaipėda Strait); N_t—number of all tagged eels. MS for eels released upstream the Kaunas HPP was calculated only for eels which had passed the HPP. The fate of eels not registered in the Nemunas Delta or Klaipėda Strait remains unknown; these eels were omitted from analysis of migration speed.

The speed of long term downstream migration (V_{long}) was calculated as time spent to cover the distance between the release site and the receivers installed in the Nemunas Delta or in the Klaipėda Strait and expressed as km/day. The speed of transient migration (V_{tran}) was calculated in the Nemunas Delta and Klaipėda Strait as the time lag between the first detection of a tag by the first and last receivers (5 km distance in the Nemunas River and 4.6 km in the Klaipėda Strait). Fulton's condition factor (*K*) representing the condition of the eel was calculated as described by Ricker (1975). River slopes between eel release sites and the Lagoon were taken from the Lithuanian rivers dataset (Jablonskis, 1962).

Data for eel migration speed, *K* and the distance between the release site and the Baltic Sea were not normally distributed (Shapiro–Wilk's *W* tests, $p < .05$), the non-parametric Mann–Whitney test was used to test for differences in parameters between the eels released in to dammed and free-flowing rivers. Simple linear regression was used to test the effect of distance of release site from the sea, eel length, river slope and *K* on the speed of downstream migration. Fisher's exact test was used to test eel MS differences between dammed, free-flowing rivers and the Curonian Lagoon.

3 | RESULTS

Mean length ranged between 94 and 51 cm, among the 63 eels that were released into four different rivers (Table 2). Mean weight of these eels ranged between 224 and 1,847 g, and mean *K* between 0.12 and 0.24. Three of these eels were determined to be males at silvering stage MII, 10 eels were females at silvering stage FIV, and the remaining 50 eels were females at silvering stage FV (Table 2).

3.1 | Migration in free flowing rivers

Eighteen out of the 38 silver eels released into free-flowing rivers of Eastern Lithuania during May–June 2014 were never detected post-release, consequently their fate is unknown. The remaining 20 eels successfully migrated downstream and reached the Nemunas Delta; MS = 52.6% (Table 3). Mean V_{long} (±*SD*) of these eels was 10.7 ± 10.7 km/day (range 2.6–46.0 km/day). Migration lasted 77 ± 47.4 days on average (range 8–151 days) to reach the Curonian Lagoon after release.

There were no significant differences ($p > .05$) in mean length, *K* and the distance from the release site to the Baltic Sea between eels released to free-flowing rivers that reached the Nemunas Delta and those which apparently did not.

3.2 | Migration in dammed river

Out of 25 eels released upstream of the Kaunas HPP, 21 (84%) moved downstream through the turbines and were detected below the HPP. Twelve eels migrated within 24 hr after release, while nine eels delayed passing through by one to 47 days. Four tagged eels did not migrate downstream and stayed in the Kaunas Reservoir until at least when the transmitter battery became discharged. Their fate remains unknown. Absence of a fish ladder at HPP means that all eels must pass directly through the turbines. Out of the 21 eels which migrated through the HPP, 11 were detected in the Nemunas Delta (MS = 52.4%) (Table 3). Mean V_{long} (±*SD*) of these eels was 13.6 ± 12.0 km/day (range 1.5–35.3 km/day). Migration lasted 59 ± 66.7 days on average (range 6–144 days) to reach the Curonian Lagoon after the release.

There was no significant difference ($p > .05$) between the V_{long} of eels released in free-flowing and dammed rivers.

3.3 | Migration within the Nemunas Delta

In the rivers of Eastern Lithuania, most of the tagged eels ($N = 54$, 86%) were released during late May–early June and nine eels (14%) were released in September. Thirty-one eels (49.2% of all eels released) were detected migrating through the Nemunas River Delta:

one eel (3%) arrived in May, five eels (16%) were detected in June, eight (26%) in July and one (3%) in September. The majority ($N = 15$, 49%) were detected in October and the one remaining (3%) was detected in November.

V_{tran}, estimated within the Nemunas Delta was 67.2 ± 39.9 km/day (range—from 1 to 124 km/day) which was significantly ($p < .05$) higher compared to V_{long} in rivers.

Most ($N = 22$; 71%) eels in the Nemunas Delta were actively migrating between 1 hr after sunset and 4 hr before sunrise. Nevertheless, seven (22.5%) eels migrated within a few hours before sunset or after sunrise; and the remaining two eels (6.5%) were detected migrating around midday.

Scanning in smaller rivers (Neris, Žeimena and Siesartis), adjacent lake and section of Nemunas River below the Kaunas HPP did not result in detection of any eels, so the fate of 32 tagged eels (50.8%) remains unknown.

3.4 | Migration in the Curonian Lagoon and Klaipėda Strait

Out of 31 eels, which were detected entering the Curonian Lagoon, at least four (13%) were caught in fyke nets by fishermen. Until the end of transmitter battery operation, 22 eels (MS = 71%) were detected in Klaipėda Strait prior to entering the Baltic Sea, while the fate of the remaining 5 eels (16%) remains unknown. The mean V_{long} in the Lagoon was estimated to be 14.6 ± 16.9 km/day (range 0.5–66.5 km/day). V_{long} (in the rivers, in the Lagoon and total [rivers + lagoon]) was not significantly correlated with distance of the release site from the Baltic Sea, river slope, TL or K. Also, there was no significant difference ($p > .05$) between the mean V_{long} in rivers (11.6 ± 11.1 km/day) and the Curonian Lagoon (14.6 ± 16.9 km/day).

The V_{tran}, estimated in the Klaipėda Strait was 35.6 ± 25.8 km/day (range from 0.4 to 78.8 km/day). There is no significant differences ($p > .05$) between mean V_{tran} in the Nemunas delta and in the Strait, however V_{tran} was significantly ($p < .05$) higher compared to V_{long} in rivers and in the Lagoon.

The peak period of eels entering the Baltic Sea was observed during late fall: 18 eels (82%) were detected in the Klaipėda Strait during October-November while the remaining four eels were detected once each in June, July, December and January, respectively.

4 | DISCUSSION

Migration successes and mean migration speed among silver eels performing downstream migrations in free-flowing and dammed rivers was found to be similar. Eel migration speed estimated during the current study was considerably lower compared to those reported elsewhere. Previously reported migration rates in regulated rivers have been highly variable, ranging between 17.3 (Klein Breteler et al., 2007), 29.4 (Breukelaar et al., 2009), 53 (Verbiest, Breukelaar, Ovidio, & Belpaire, 2012) and 64.8–93.6 km/day (Tesch, 1994). Data on eel migration speeds in free flowing rivers are scarce, but Simon et al. (2011) reported mean migration speeds for different eel groups that varied between c. 5 and 70 km/day, while Bultel et al. (2014) reported a mean migration speed of 4.5 km/day. Prior to entering the Baltic Sea, eels pass through the highly eutrophic Curonian Lagoon. The V_{long} in the Lagoon was slightly faster when compared with migration speeds in rivers, but these differences were not statistically significant ($p > .05$). Speed of downstream migration was independent of eel body length in rivers and in the Lagoon, consistent with results reported by Haraldstad, Vøllestad, and Jonsson (1985), but in contrast with the conclusion of Bultel et al. (2014) that migration speed was correlated with total length and body weight. The lower migration speeds observed in the current study might be related to seasonal differences among eel spawning migrations. Downstream runs of silver eels in Western Europe typically start in autumn (Bruijs & Durif, 2009), yet along the South-Eastern Baltic coast, most intense spawning migrations start in early March and last until late May (Ložys et al., 2008). The earlier commencement of downstream migration has led to an assumption that eels enter the sea earlier as a consequence, but the results from the current study demonstrated that a majority of migrating eels caught in streams during spring did not enter the Baltic Sea until late autumn (October–November). It was suggested that spawners start their migrations from distant areas (e.g., Lithuania) earlier (in spring) (Bruijs & Durif, 2009). In contrast, more recently Righton et al. (2016) demonstrated that "the timing of autumn escapement and the rate of migration are inconsistent with the century-long held assumption that eels spawn as a single reproductive cohort in the spring time following their escapement from European waterways. They suggested that European eels adopt a mixed migratory strategy, with some individuals able to achieve a rapid migration, whereas others arrive only in time for the following spawning season". This may well explain the large differences in the speed of downsream migration observed during the current study where eels were migrating within a range of 1.5–46.0 km/day. Slow migration speed during the continental migration phase suggests that eel migration in this study was accompanied by long pauses. This is possibly due to longer stopovers for feeding (some eels at silvering stages SFV and SFIV were found to be feeding during downstream migrations (J. Dainys, unpubl. data; Westin, 2003)) and as suggested by Durif, Dufour, and Elie (2005) unfavourable weather conditions for migration in summer (e.g., calm weather, reduced flow velocity) might substantially reduce the rate of eel migration. In line with previous observations (Lowe, 1952) increased migration activity in the current study was observed during less-illuminated phases of the lunar cycle—most of the eels (81%) actively migrated during first and third quarter of the moon, whereas only 13% and 6% were recorded during the new and full moon, respectively. However, some recent studies have reported lunar phase had no significant influence on eel migration (Reckordt, Ubl, Wagner, Frankowski, & Dorow, 2014). Stein et al. (2016) reported that eels tagged in upstream river reaches were less likely to complete their migration and tended to dwell longer in the river system than eels that were tagged in the lower reaches. In contrast the current study showed no effect of eel release site or river slope on either migration speed or migration success. Moreover, previous studies (e.g., Aarestrup et al., 2008; Simon et al., 2011) have also demonstrated that some eels suspend their autumn migration to resume it during the following spring or autumn and in this way take more than a year to reach the outlet of even smaller rivers, or sometimes even revert from silver to yellow eel stage and cease migration (Durif et al., 2005; Stein et al., 2016; Svedäng & Wickström, 1997). It follows that overall downstream migration success is likely to be higher than was observed if some eels resumed their downstream migration after their tag transmitter batteries had discharged.

Previous behavioural studies (Boubée & Williams, 2006; Calles et al., 2010; Durif, Elie, Gosset, Rives, & Travade, 2003; Pedersen et al., 2012) suggested that HPPs and dams may have indirect negative effects on eel migration: eels often delay their passage through an obstruction and consequently their migration period becomes extended. Results of the current study partly support this observation as 36% of eels released upstream from the Kaunas HPP also delayed passing through the turbines for periods from one to 47 days, while 16% of eels did not migrate at all. The remaining eels passed through the turbines of the Kaunas HPP within 24 hr after their release. After the eels passed through the HPP only five transmitters (23.8%) were detected as stationary in the proximity of the Kaunas HPP within the period until the transmitter battery was exhausted (these eels presumably suffered lethal injuries), while more than half of all eels (52.4%) that passed through the turbines of Kaunas HPP were detected in the Nemunas Delta. The fate of the five eels (23.8%) remains unknown.

During downstream migration no eels were exposed to commercial fishing (except in the Lagoon) because they were released downstream of licensed fishing sites. The impacts of predation, recreational angling, poaching or other sources of mortality are nevertheless unknown. Scanning with boat-based receivers in the rivers, an adjacent lake, and the section of Nemunas River below the Kaunas HPP did not result in detection of any eels. Presumably the missing eels were either caught by anglers or predators and their tags were taken away from the river, or the eels stayed somewhere in the Nemunas River below the scanned reaches, or perhaps entered small tributaries of the main rivers and were missed during active scanning.

After downstream migration 31 eels entered the Curonian Lagoon. Despite fishing and predation pressure in the Curonian Lagoon being markedly higher (Pūtys, 2012) compared to rivers, the migration distance in the Lagoon was substantially shorter (c. 50 km) and the success rate of migration through the Lagoon was considerably higher. Relatively high migration success in the Lagoon might also be explained by eels reaching the Lagoon at the end of the continental migration phase and, as suggested by Righton et al. (2016), had adopted a rapid migratory strategy, such that most of these eels ($N = 22$) did not cease their migration through the Lagoon. Migration strategies of the four eels caught by fishermen and the five eels whose fate is unknown (they might also have been caught but not reported) remain unclear.

In line with previous findings of Brown, Haro, and Castro-Santos (2009) more than two-thirds of all eels actively migrated through the Nemunas River Delta during the night time—between 1 hr after sunset and 4 hr before dawn. However, some eels were detected migrating during the daytime or even at midday, especially in the Klaipėda Strait. Vøllestad and Jonsson (1986) and Durif (2003) suggested that eel migration during the daytime is related to increased water turbidity and rate of water flow. Water turbidity in the Curonian Lagoon is generally very high and the depth of Klaipėda Strait is c. 15 m, leading to presumed low illuminance conditions at the bottom, which might explain why 10 out of 22 eels migrating through the Lagoon to the Sea emigrated during the daytime. Eels entered the Baltic Sea when the water temperature was 5.1–10.1°C, which is within the optimal range reported for eel migrations (Vøllestad & Jonsson, 1986).

Overall migration success in the current study was 35%, but actual escapement success might be higher, because some tagged eels were never detected after release yet might have reached the Baltic Sea after their transmitter batteries had expired. Our results are consistent with those previously reported for eel migration success rates in regulated rivers, which are highly variable ranging from 10% to 37% (Marohn, Prigge, & Hanel, 2014; Verbiest et al., 2012; Winter et al., 2006). Eel migration success beyond their entry into the Baltic Sea remains unknown. This study highlights that production of spawners for any stock restoration endeavours needs to be calculated with caution by estimating not only impact of HPP but also other possible sources of mortality.

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IV.

Are Lithuanian Eels, *Anguilla anguilla* (Linnaeus, 1758), Fat Enough To Reach The Spawning Grounds?

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Abstract

Stocks of the European eel *Anguilla anguilla* have been in a steep decline since the 1980s. Stocking of water bodies with juvenile eels captured in the wild to establish or enhance local populations has been a common practise in Europe for many decades. However, the degree of contribution by stocked eels to natural spawning capacity is poorly known and extensively debated. There have been suggestions that eels derived from stocking are less likely to contribute to the spawning stock due to a lack of navigational capability and lower fitness related to insufficiency of energetic resources. Results of the current study indicated that eels translocated long distances from the point of capture and released into inland waters in Lithuania are successfully undergoing the silvering process. A proportion of 23.7% (N = 27) among all migrating eels were described to be at the yellow (SI, SFII or SFIII) eel stage and downstream movements of these eels should be attributed to local movements, rather than spawning migration; 76.3% were assigned to the silver eel stage. This study suggests that 36.8% (N = 32) of downstream migrating silver eels of stocked origin had accumulated sufficient energetic resources for spawning migration and gonadal development and should be able to traverse the 7900-km distance to the presumptive spawning grounds in the Sargasso Sea. The rest of migrating silver eels (63.2%, N = 55) had insufficient energetic resources; the average potential swimming range of these eels was estimated to be 6135 ± 683 km.

Key words: *Anguilla anguilla*, spawning migration, silvering, energetic resources, fat content.

Introduction

Since the 1980‘s, for reasons that remain unknown, steep population declines have been observed over the entire range of European eel (*Anguilla anguilla*) distribution: estimates of decline in rates of recruitment range from 50% to 99% (Moriarty and Dekker 1997; Feunteun 2002; Dekker 2004; ICES 2010; Jacoby and Gollock 2014). In the Baltic, recruitment of yellow eel has been continuously in decline since the 1950‘s, and a decline by 90% occurred, when comparing with recruitment level observed in 1960–1979 (ICES 2011). Landings have also decreased in many parts of the Baltic. For example, landings in the Curonian Lagoon show a 90% decline compared to pre-WW2 landings (ICES 2011). In response to declines in eel stocks the European Union (EU) issued the Regulation of European Council No. 1100/2007 during September 2007, which lays down measures for stock restoration of European eels. In accordance with regulations as well as national eel management plans developed by member states, many European countries are releasing wild caught glass or aquaculture-reared eels into coastal and inland waters in order to enhance the production of adult (silver) eels escaping to the sea for spawning migration (ICES 2014). After several years or even decades spent in fresh or brackish waters these stocked eels reach the silver eel stage and start their spawning migration (Prigge et al. 2013; Simon and Dörner 2014), however, the degree of contribution to the spawning stock from those eels is poorly known (Limburg et al. 2003).

Eels are often stocked at the glass eel stage; these eels are usually transported as freight prior to release (Bogdan and Waluga1980). Sometimes such transportation involves long distances; e. g. glass eels are shipped over 2000 kilometres from United Kingdom or France to the North-Eastern area of the species distribution range in Lithuania. Although it has been estimated that 80% of eels inhabiting Curonian lagoon and 98% of eels in coastal waters have recruited naturally (Lin et al. 2007; Ložys et al. 2008), evidences of previous studies shows that all eels inhabiting Lithuanian inland waters originate from the release of cultured stock (Shiao et al. 2006; Lin et al. 2007; Ložys et al. 2008, Ragauskas et al. 2014). Even after WWII when the population was generally in good condition, eel abundance in the Eastern part of Lithuania was extremely low and largely depended on pre-war releases during 1928-1939 (Anonymous 1976). Eel stock in eastern Lithuania was built again after stocking programmes were started in 1956. During the last decades there is no information about eel caught in water body which is not stocked or connected via river with such lake.

There have been suggestions that eels derived from aquaculture farms are less likely to contribute to the spawning stock. Consequently, the rationale of re-stocking with farmed eels as an approach to mitigating decline in wild eel populations is increasingly being questioned (Brämick et al. 2016). Simon and Döner (2014) found that wild-sourced European glass eels showed better overall performance of survival, growth and condition compared with farm-sourced eels over a 7-year study period after stocking. Moreover, Couillard et al. (2014) demonstrated that none of the American silver eels (*Anguilla rostrata*) of farmed origin that were migrating downstream had enough energetic reserves (fat content) to complete both migration and maturation, whereas 57% of the silver eels of natural origin had adequate reserves.

Migrating silver eels at the final silvering stage do not feed during their migration to the spawning grounds (Tesch 2003); therefore they completely rely on accumulating sufficient fat stores during the sedentary yellow eel stage spent in coastal or inland waters to obtain energy for migration and gonad development (Tesch 2003). The migration distance to the presumed spawning areas is at least 4000 km, but from different areas of the species' range may differ up to more than 3500 km (Schmidt 1923; McCleave 1993; Clevestam et al. 2011). Eels migrating from the North-Eastern region of their distribution range obviously need more energetic resources and more time to reach the spawning grounds in the Sargasso Sea, compared to eels migrating from the Atlantic coast bordering Eastern Europe. Spawning migration from the Western part of Europe is estimated to be c. 5000 km (Van Ginneken et al. 2005; Aarestrup et al.2009), whereas from the inland waters of Eastern Lithuania migrating eels must cover almost 8000 km. Due to a lack of data about energy resources among stocked eels migrating to spawn, especially from the North-Eastern region of the species' natural distribution range, it is unclear if European eels translocated over long distances prior to stocking have sufficient capacity to accommodate the extended distances of migration caused by human intervention. Inability of stocked eels in North America to accumulate adequate fat reserves for migration and reproduction was reported by Couillard et al. (2014).

This study was conducted to reveal whether or not eels translocated from the coasts of Western Europe to the North-Eastern edge of their distribution range can accumulate enough energy for c. 7900 kilometre long spawning migration to the spawning grounds presumably located in the Sargasso Sea and gonadal development.

2. Materials and Methods

2.1. Eel sampling design and technique

During annual downstream migrations in April–November of 2014–2016, an aggregate of 114 eels were caught via a trap net of 5–8-mm mesh size, from 10 different rivers (Alauša, Kretuona, Lakaja, Metelytė, Peršėkė, Riešė, Siesartis, Spernia, Žeimena, Žežiebra) in the Eastern and Southern parts of Lithuania, (Fig. 1 and Table 1) . All eels were collected in rivers outflowing from mesotrophic lakes. The most intensive spawning migrations downstream in north-eastern eel distribution range generally occur during spring, most of the samples (N=77) were collected in April, May and June, eight eels were caught during summer time in July and August, while the rest 29 eels were caught during October, November and December. Such sampling distribution in time scale is in line with previously reported eel migration patterns in Lithuania, when c. 60% of eels start their migration in spring, 10% in summer and rest 30% in autumn (Ložys et al. 2008). All sampled eels were euthanized immediately after capture applying a lethal blow to the head. Eels were stored at -22°C in a freezer until the laboratory analysis of their fat content. To avoid weight loss the eels were stored in vacuum packaging. The surface areas of lakes where the ongrown eels have been released and allowed to grow before being caught during their migration ranged from 0.6 to 23.3 km^2 in surface and 4.0 to 15.2 m in depth (Table 1). Waters temperature varied between 12–19°C and dissolved oxygen 8.3–11.5 mg L^{-1} in inverse proportion temperature among the lakes (Table 1.).

Fig. 1 Map of Lithuania depicting the ten sites sampled for eels during this study

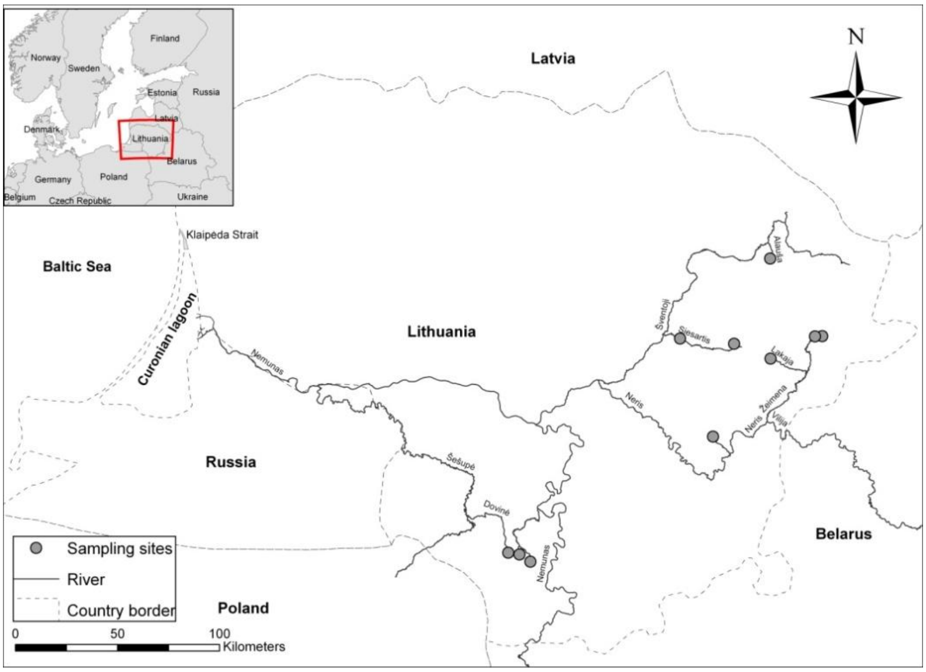

Table 1 Hydromorphological and physico-chemical characteristics of Lithuanian lakes, stocked with eels, outflowing to sampled rivers: surface area, mean depth, water temperature (T), dissolved oxygen (O_2), total phosphorus and nitrogen (TP, TN) and chlorophyll *a* (Chl. *a*). Concentrations of chlorophyll-a were measured by a spectrometer in accordance with the ISO 10260:1992 standard. Multiannual averages of physico-chemical characteristics were compiled from available annual (spring−autumn) averages provided by the Lithuanian Environmental Protection Agency (http://vanduo.gamta.lt/cms/index?rubricId = 8ea41f73-9742-4d71-aa10-0a5988713fe5, accessed on 2016-05-26)

Sampled river	**Coordinates, WGS**	**Stocked lake**	**Surface area, km^2**	**Mean depth, m**	**T, °C**	**O_2, mg L^{-1}**	**TP, µg L^{-1}**	**TN, µg L^{-1}**	**Chl. *a*, µg L^{-1}**
Žežiebra	55.232243, 25.39934	Dūriai	2.7	4.0	11.9	11.5	25	1010	12.1
Kretuona	55.270707, 26.081396	Kretuonas	8.6	5.2	16.9	8.3	18	459	4.8
Alauša	55.636321, 25.698559	Alaušas	10.7	11.9	15.5	9.2	7	660	2.5
Metelytė	54.331091, 23.747907	Metelys	12.9	6.8	16.8	9.2	29	775	4.2
Peršekė	54.329241, 23.829165	Obelija	5.7	4.5	17.9	9.4	34	1225	6.5
Lakaja	55.1814, 25.678833	Juodieji Lakajai	3.9	8.2	17.7	10.1	11	488	7.9
Siesartis	55.287674, 24.933283	Siesartis	5.0	11.3	16.0	10.2	9	858	2.5
Spernia	54.337942, 23.664945	Dusia	23.3	15.4	16.2	9.9	34	763	5.7
Žeimena	55.254464, 25.996888	Žeimenys	4.4	6.9	18.5	9.4	26	383	7.6
Riešė	54.785018, 25.329406	Balsys	0.6	15.2	17.5	10.1	16	550	8.2

2.2. Silvering stage determination

Morphometric measures (total body length and weight; gutted weight; height and width of the eye and length of the pectoral fin) were made on fresh carcasses immediately after euthanasia. Sex was determined by morphological examination of the gonad (Tesch 1977), aided by a stereoscopic binocular microscope for smaller eels. The silvering index is based on the following external body measurements: total body length (TL), body weight (M), pectoral fin length (LPF), and mean eye diameter (MD = [vertical eye diameter + horizontal eye diameter]/2) and was determined as described in Durif et al. (2005, 2009). It allows determination of the 'degree of silvering': SI-SFII are 'yellow' eels (SI - sexually undifferentiated); SFIII eels are pre-migrant females; SFIV and SFV are the last silvering stages for 'silver' females, and SMII is the last silvering stage for 'silver' males.

2.3. Determination of fat content

A section of lateral muscle from both sides of the body, 2.5 cm away from the anal vent, was removed for the analysis of muscle fat content (the total lipid content of the muscle). Soxtec method (Gerhardt Soxterm fat extraction system, Germany) was used to extract lipids from the sample (Anderson 2004). A sample of about 25–35 g of muscle tissue was homogenised. The proteins were digested by boiling the sample in hydrochloric acid (4M aquatic solution) for one hour to break the lipo-protein bonds. The solution was then filtered, and fats remaining on the filter were dried at 103°C for 20 minutes in a mechanical convection oven and then extracted with 150mL of petroleum ether, boiled for 90 min at 150°C and rinsed for 60 min. After fat extraction, the samples were dried at 103°C for one hour in a mechanical convection oven and weighed to the nearest 0.001 g. Muscle fat content (%) was calculated as the ratio of the initial sample weight and its weight after the treatment. The individual fat reserve (M_{fat}, g) wascalculated as described by Couillard et al. (2014):

$$M_{fat} = 10^{-2} \times \%\ lipid\ body\ mass \times 0.8\ \ skin\ and\ bone\ excluded\ \ .$$

2.4. Calculation of swimming potential

Swimming potential was calculated according to Van Ginneken and Van den Thillart (2000). These authors suggest that 60% of the lipids are reserved for gonadal development, the caloric value of eel fat is 10.68 kcal g^{-1}, and the energy cost of swimming for eels is 0.137 Cal g^{-1} km^{-1} (using wet weight). The distance of migration from inland waters in Eastern Lithuania to presumed spawning grounds in the Sargasso Sea was estimated to be c. 7900 km based on Clevestam et al. (2011) who estimated the distance from Öresund in Sweden to be c. 6900 km. 1000 km were added for the eels to reach Öresund from the sampling sites via the Klaipėda Strait, which is the gateway to the marine environment for most migrating eels from Lithuanian inland waters (Fig. 1). Silver eels of different silvering stages (SMII, SFV and SFIV) were not pooled during the analysis because eels in the last silvering stage

(SMII and SFV) are known to cease feeding (Van den Thillart and Dufour 2009), whereas SFIV eels are still able to increase their fat stores. The swimming potential for yellow eels (SI, SFII and SFIII) was not calculated as these eels only undertake local movements but not spawning migrations.

2.5. Statistical analysis

The relationship between the silvering stage and fat content was determined using correlation analysis. As only 7 male individuals were caught (SMII), the correlation analysis was conducted on a dataset of undifferentiated and female eels (SI–SFV). Pearson's correlation test was used and silvering stage variable was log-transformed. One-way analysis of variance (ANOVA) was followed by generalised Tukey's HSD post-hoc tests (for the case of unequal sample sizes) to indicate homogenous stage groups (the assumption of homoscedasticity among data was met (Levene's tests: $P>0.08$)). The analysis was conducted using the statistical software package STATISTICA® 8.

2.6. Ethics statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All animal work was conducted on public land and waterways, and complied with relevant national and international guidelines and legislation. Annual field permits to perform fish surveys (for collecting eels from Lithuanian rivers) were issued by the Environmental Protection Agency under the Ministry of Environment of the Republic of Lithuania for the duration of this 3-year study (No. 025 (2014); No. 016 (2015); and No. 002 (2016)). These permits covered all specific procedures carried out in the current study, including sampling locations, duration and method.

No additional permits were required as no laboratory experiments involving live animals were performed. An Animal Ethics Committee (AEC) of the Nature Research Centre was only recently established on 17 May 2016, whereas the current study was performed during April 2014 – May 2016, preceding the existence of the AEC.

3. Results

3.1. Maturation stage and sex structure

The majority of eels sampled (65.8%, N = 75) were at the last silvering stage (SFV for females or SMII for males), whereas eels of stage SFIV accounted for 10.5% (N = 12). The yellow eels (stages SI, SFII and SFIII) accounted for 23.7% (N = 27) of all eels sampled. Females dominated the samples, accounting for 88% (N = 100) of all the eels that were analysed. Smaller bodied males accounted for 6.1% (N = 7), whilst another 7 individuals (6.1%) were sexually undifferentiated young yellow eels.

3.2. Energetic resources and swimming potential

The results of total fat content analysis showed that there was a significant correlation between the silvering stage and fat content ($r = 0.80$, $P < 0.001$), although up to 40% variation in fat content would be due to other unspecified explanatory factors i.e. $r^2 = 0.63$. ANOVA also indicated a significant stage effect on fat content ($F_{5,108} = 62.5$, $P < 0.001$), and post-hoc tests separated the eels into four homogenous groups: SI, SFII, SFIII-SFIV-SFV and SFIV-SFV-SMII ($P < 0.02$). Migrating male eels of the latest SMII silvering stage had the highest muscle fat content, varying from 28.5 to 33.9% (31.0 ± 1.9%, mean ± SD) with their swimming potential varying from 7987 to 8462 km (8152 ± 174km, mean ± SD), while the females of the latest (SFV) silvering stage had an average fat content of 26.3 ± 3.7 with average swimming potential of 6743 ± 1116 km.Eels at silvering stage SFIV had an average fat content of 26.3 ± 2.7%. The average swimming potential of these eels was equivalent to 6798 ± 976km. The yellow eels possessed lower percentages of fat content – SFIII and SFII eels had 25.1 ± 2.8 and 17.6 ± 4.6% average fat content, respectively. The yellow eels at the silvering stage SI had the lowest fat content (average 4.6 ± 1.9%).

The analytical results suggested that 100% (N = 7) of male eels of the latest silvering stage SMII and 30.9% (N = 21) of female eels at the latest silvering stage SFV possessed sufficient fat reserves to be capable of migrating from Lithuanian coastal waters to the Sargasso Sea (>7900 km). The remainder 69.1% (N = 47) of the female eels at stage SFV had insufficient energy resources to complete the migration. Four out of 12 (33.3%) eels sampled at the silvering stage SFIV had sufficient energy resources for spawning migration (Table 2).

Table 2 The main morphometric parameters, fat content and swimming potential of eels sampled from Lithuanian waters

Silvering stage	N	Length, cm	Weight, g	Fat content,%	Swimming potential, km
SI	7	28.0 ± 8.8	39 ± 32	4.6 ± 1.9	NA
SFII	5	56.2 ± 5.4	254 ± 64	17.6 ± 4.6	NA
SFIII	15	70.7 ± 8.2	593 ± 224	25.1 ± 2.8	NA
SFIV	12	89.5 ± 7.1	1418 ± 303	26.3 ± 2.7	6798 ± 976
SFV	68	70.4 ± 8.9	634 ± 231	26.3 ± 3.7	6743 ± 1116
SMII	7	48.0 ± 7.8	194 ± 142	31.0 ± 1.9	8152 ± 174
SFV and SMII	75	68.3 ± 10.9	593 ± 2582	26.7 ± 3.8	6874 ± 1141

The regression model for fat content of SI–SFV eels as a function of stage and chlorophyll *a* is presented in Table 3. It indicated that stage was the only significant predictor of eel fat content, whereas the coefficient for chlorophyll *a* was not significant.

4. Discussion

Our study results suggest that at least 37% of glass eels translocated by freight for more than 2000 kilometres from the United Kingdom or France and then released into Lithuanian inland waters at the final silvering stage (SFV and SMII) accumulate sufficient energetic stores of fat for gonadal development and spawning migration of c. 7900 km to the Sargasso Sea. The remaining 63% of eels at the final SFV and SMII silvering stages had insufficient fat stores, with average shortage of 2.5 ± 0.9%. Eels of the last silvering stage (SFV or SMII) accounted 86% (N = 75) of all silver eels (SFIV, SFV and SMII) performing downstream migrations. Four out of 12 eels at the SFIV silvering stage had enough energetic resources to reach the spawning grounds, while the remaining eight eels were unable to successfully undertake the spawning migration due to insufficient energetic resources and a swimming potential that was too low to cover a distance longer than 7900 km. The remaining 27 eels in our study were described to be in the yellow (SI, SFII or SFIII) eel stage with relatively low fat content (18.4 ± 9.3%). Swimming potential of these eels was not calculated, due to downstream movements of these eels could be linked to local movements, rather than actual spawning migration (Ovidio et al. 2013; Cobo et al. 2014). Despite yellow eels (SI-SFII) belonging to a life history category that is considered as a resident stage that does not engage in spawning migrations, Belpaire et al. (2009) suggested that the decrease in fat content in yellow eels may be a key element in the decline of stocks which raises serious concerns about the chances of the stock to recover. Decreases in the mean lipid content of yellow eels (from c. 21 to 13%) over a 30-year period have been observed in the Netherlands (De Boer et al. 2010), while very similar decreases (from 20 to 12%) have also been reported in Belgium between 1994 and 2006 (Belpaire et al. 2009). In contrast to previous findings, Oliver et al. (2015) reported increased fat content of yellow eels (mean fat content = 21% in 1986; and 37 % in 2004–2008) caught in different locations in Scotland, however these authors agree that 37% is an unusually high fat content for yellow eels. Maes et al. (2007) reported a mean fat content of 14.9% for yellow eels collected in Flanders, and McHugh et al. (2010) reported fat content to be ranging between 8.28 and 9.18% for mixed sex samples of silver eels taken from Irish waters. In Lithuania's case there are no historical data on yellow eel fat content, but the mean fat content of yellow eels (18.4%) measured in this current study was relatively higher when compared to quantities reported by Maes et al. (2007), Belpaire et al. (2009), De Boer et al. (2010) and McHugh et al. (2010). This suggests that stocked Lithuanian yellow eels are of good quality.

Even after decades of research, eel orientation mechanisms and migration routes to the presumptive spawning grounds that cover a vast area of more than 1.7×10^6 km^2 remain a mystery (Béguer-Pon et al. 2016). Moreover, anguillids are known to perform diurnal vertical migrations (Aarestrup et al. 2009; Beguer-Pon et al. 2012). Diel vertical migration in the field (200–700 m) may result in higher efficiency at greater depth and pressure during the day, however temperatures at 700 m in the open ocean are around 6°C and it remains unknown whether silver eels are capable of swimming at such low temperatures (Palstra and Van den Thillart 2010). In this context, assessing the role of oceanic currents during the silver eel's migration appears to be potentially very important, but it has never been quantified (Béguer-Pon et al. 2016). Given these uncertainties regarding migration, calculation of energy demand for successfully reaching the Sargasso sea to spawn should be considered as a rough approximation at best and inadequate for drawing firm conclusions. Nevertheless, Lithuania is in the North-Eastern part of the European distribution range for eels, which is among the most distant regions from the presumptive eel spawning grounds in Sargasso Sea. It is known that in such distant areas from northern latitudes eel migration commences earlier (Bruijs and Durif 2009). This phenomenon is associated with species adaptation to reach spawning grounds in synchrony with eels from different areas of the distribution range (Bruijs and Durif 2009). Critically, it also enables them to feed during the early continental migration phase, especially in the Lithuanian case when passing through the highly eutrophic Curonian Lagoon that provides a rich food supply prior to entering the Baltic Sea. Aarestrup et al. (2008) reported that in Denmark the migration of silver eels may not always be a direct journey to the ocean, but may also include resident periods in coastal areas. Some of SFV and SFIV eels in the current study were similarly found to be feeding (the stomachs of 7 eels were filled with various marginally digested food items, e.g. insect larvae and small fish). Moreover, Svedäng and Wickström (1997) suggested that silver eels at the non-feeding stage with commensurate low fat content may temporarily halt their migration, revert to a feeding stage, and “bulk up” until their fat reserves are sufficient to carry out successful migration to the spawning area. Westin (1990) reported that tagged sea-running silver eels have been recaptured in the Baltic Sea after more than 4 years. This supports the idea that silver eels, especially at early silvering stages, are likely to be able to resume feeding during migration. Sjöberg et al. (2016), however, reported, that some of the migrating silver eels recaptured after overwintering lost their weight, nevertheless at least some of the eels were feeding. Despite weight loss, stored energetic resources were not examined as well as silvering stage was determined using ocular index only. Thus it remains unclear do those eel were at the final or early silvering stage and what shortage of energetic resources they had, if any. Moreover, Sjöberg et al. (2016) suggest that the weight decrease may not be associated with a migration failure but instead be a result of the maturation process where, for example, muscle tissue is replaced by fat.

Svedäng and Wickström (1997)showed that fat reserves among migrating silver eels ranged from 10 to 28%, which suggests that most Swedish silver eels of stocked origin cannot complete the journey to the spawning grounds. However, Van Ginneken and van den Thillart (2000) argue that mature females leaving the coasts of Europe have sufficient energy reserves to swim c. 6000 kilometres to the Sargasso Sea. Substantial individual variation in fat content among silver eels of unknown origin has been reported from a study of a lake in Norway: in this instance the eels contained between 12.5 and 41.9% fat (Bergersen and Klemetsen 1988). Clevestam and Wickström (2008) reported that silver eels of natural origin had higher fat content and exhibited a higher degree of maturity when caught during their migration out of the Baltic Sea compared with silver eels of stocked origin. Similar results were obtained when silver American eel (*Anguilla rostrata*) eels of stocked origin exhibited lower values of silvering indices (Couillard et al. 2014). Clevestam et al. (2011) suggested that a large proportion of female silver eels (at least 26.4%) from the Baltic Sea catchment area will have inadequate or suboptimal reserves for successful migration and reproduction, but the origin of these eels was not identified. Limburg et al. (2003) noted that silver eels exiting the Baltic Sea had a higher fat content (21.1% of body weight) than those collected in the Southern Baltic near Denmark (18.6%), but differences were not significant between native eels and those presumed to have been stocked within the same geographic area. There are, however, indications that silver eels departing from fresh water bodies are less mature than those in the Baltic outlet, which concurs with other studies showing a gradual transition from yellow to latest silver stages (Durif et al. 2005). Couillard et al. (2014) compared energy reserves of migrant silver American Eels *Anguilla rostrata* from a stocking program with those originating from wild recruitment. It was estimated that 100% of the stocked eels had inadequate fat reserves for migration and reproduction, whereas 57% of the natural migrants had adequate reserves. Lithuanian silver eels (SFIV, SFV and SMII) of stocked origin had c. 26-27% fat in their muscles on average when migrating downstream. However, the average fat content of silver eels that were assessed as being capable of reaching the spawning grounds was somewhat greater at 30.3%. The fat content of Lithuanian silver eels of stocked origin was similar compared to that reported for eels migrating from the western region their geographic distribution range: Mariottini et al. (2006) reported fat content of 25-27% for eels collected migrating from lagoons of Italy, but the silvering stage of these eels was not determined. The fat content of seven SFIV downstream migrating eels caught in River Frémur (Northern France) was reported to be 18.3%, while thirteen SFV eels had 20.3% fat on average (Besson et al. 2016). The average fat content for silver eels caught during migration in Northern Ireland was 26.7% for males (SMII) and 22.7% for females (SFV) (Barry et al. 2016), while McHugh et al. (2010) reported between 14.3 and 20.9% for mixed sex silver eels sampled from Irish waters. Silver eels migrating in Germany were reported to have a mean fat content of 27.3% (Marohn et al. 2014). The results of the fat analysis from the current study are consistent with results from other studies which have shown that fat content in silver eels typically varies between 25 and 30% (Bertin 1956; Boetius and Boetius 1985; Bergersen and Klemetsen 1988; Larsson et al. 1990; Tesch 2003; Clevestam et al. 2011). In contrast to the results of Couillard et al. (2014) for American eel, these studies indicated that translocation over long distances does not affect ability to accumulate adequate energy reserves.

We estimated that the 19 out of 55 (34.5%) silver eels which possessed potential to swim distances further than 6500 km, but less than 7900 km, would have needed to increase their energy resources at least by an additional 1.5 ± 0.3% to be able to reach their spawning grounds. Some among the silver eels that we sampled were found to be feeding, suggesting that eels with a minor shortage of energy resources were likely to marginally increase their muscle lipid content to an adequate level for migration. The swimming range among the remaining 36 silver eels with insufficient energetic resources was estimated to be between 4584 and 6459 km. To reach the minimum required level of energy for successful migration to spawn, they needed to increase their fat reserves by at least an additional 2.9 ± 0.7%. These eels, however, were also able to feed to potentially increase their energetic resources.

Svedäng and Wickström (1997) found no correlation between the maturity stage and muscle fat concentration among silver eels. Furthermore, testing for correlation between the muscle fat concentration, hepato-somatic and gonado-somatic indices revealed that relative liver size was unrelated to the maturation process as well as there were no correlation between fat content and maturation indices. In contrast, our study demonstrated that the correlation between maturity stage and muscle fat concentration in silver eels was significant, showing that fat concentration in muscle increased with the ongoing silvering process As all eels were collected in rivers outflowing of mesotrophic lakes our results can by applied only for mesotrophic waters.

Despite some limitations of our study it can nevertheless be concluded that more than one third of silver eels across all stages that were previously translocated for a considerable distance and then released into inland waters of North-Eastern Europe for restocking natural populations, had sufficient energetic resources for successful spawning migration and gonadal maturation. The remaining two thirds of silver eels had marginal shortages of energetic reserves, but when engaged in downstream migrations these eels were at early silvering stages and still able to feed to increase the fat reserves stored in their muscle tissue.

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