Environ Biol Fish (2018) 101:127–136
https://doi.org/10.1007/s10641-017-0686-y

Are Lithuanian eels fat enough to reach the spawning grounds?

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Received: 12 October 2016 / Accepted: 16 October 2017 / Published online: 23 October 2017

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.

Keywords *Anguilla Anguilla* · Spawning migration · Silvering · Energetic resources · Fat content

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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 Waluga 1980). Sometimes such transportation involves long distances; e.g., glass eels are shipped over 2000 km 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 Dörner (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 km long spawning migration to the spawning grounds presumably located in the Sargasso Sea and gonadal development.

Materials and methods

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

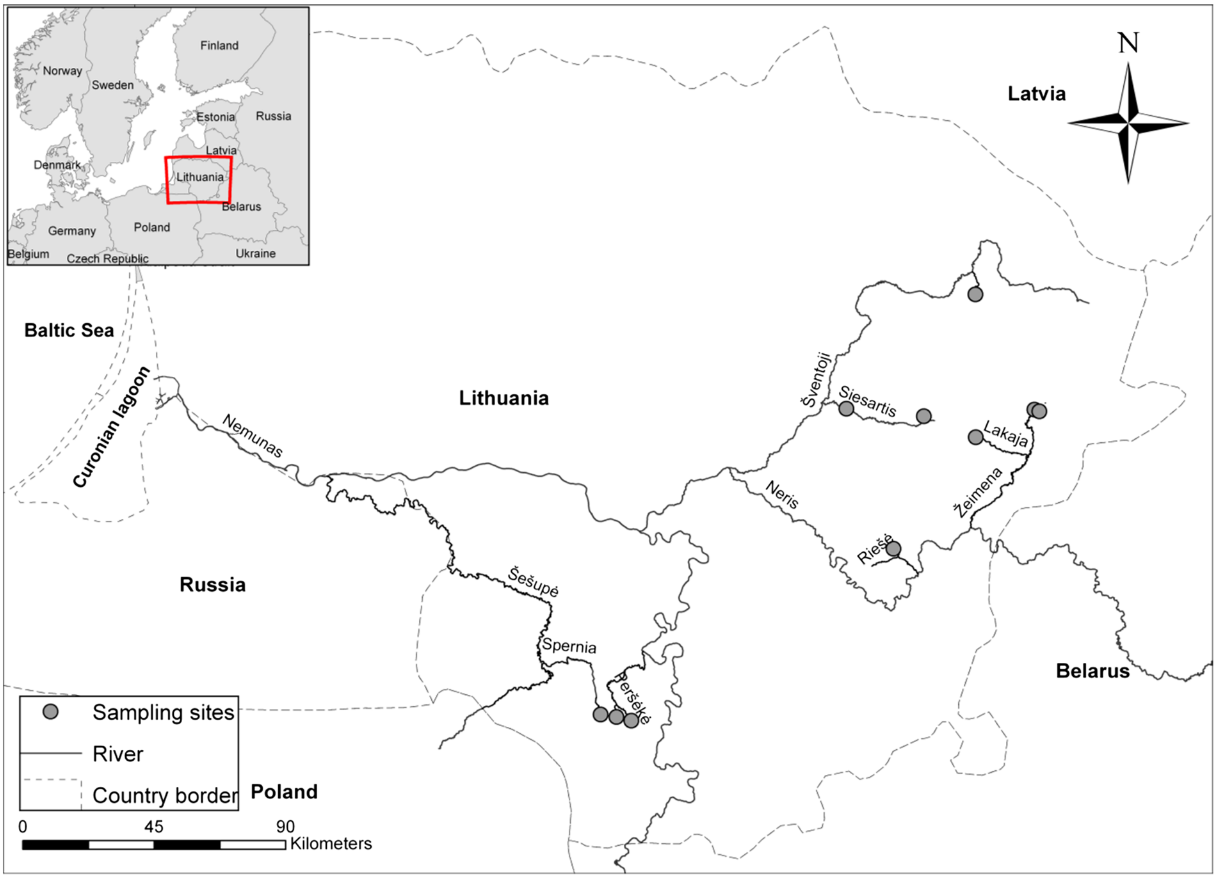

Fig. 1 Map of Lithuania depicting the ten sites sampled for eels during this study

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 and 19 °C and dissolved oxygen 8.3–11.5 mg L^{-1} in inverse proportion temperature among the lakes (Table 1).

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

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*)

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

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)

silvering stages for 'silver' females, and SMII is the last silvering stage for 'silver' males.

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 (4 M 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 min in a mechanical convection oven and then extracted with 150 mL 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):

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

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.

Statistical analysis

Relationships between the silvering stage and fat content were determined using correlation analysis. As only seven male individuals were caught (SMII), the correlation analysis was conducted on a dataset of undifferentiated and female eels (SI–SFV). Nonparametric Spearman rank correlation tests were used because some of these variables were non-linearly related to the silvering stage. The effect of lake trophic status on fat resources accumulated by eels was tested by a multiple regression of fat content on log-transformed silvering stage and chlorophyll *a* concentration, using the dataset of stages SI–SFV. The analysis was conducted using the statistical software package STATISTICA® 8.

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.

Results

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 seven individuals (6.1%) were sexually undifferentiated young yellow eels.

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 ($r = 0.41$, $P < 0.001$), although almost 80% of the fat content would be due to other unspecified explanatory factors i.e. $r^2 = 0.23$. 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 ± 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 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).

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.

Discussion

Our study results suggest that at least 37% of glass eels translocated by freight for more than 2000 km from the United Kingdom or France and then released into Lithuanian inland waters at the final silvering stage (SFV

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

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

Table 3 Multiple regression model for fat content of undifferentiated and female eels (stages SI–SFV): $F_{2,104} = 92.4$, $P < 0.001$, $R^2 = 64\%$

Parameter	$\beta \pm SE$	$b \pm SE$	t_{104}	P
Intercept		6.22 ± 1.95	3.2	0.002
Stage	0.82 ± 0.06	12.22 ± 0.93	13.2	<0.001
Chl. *a*	0.08 ± 0.06	0.21 ± 0.16	1.3	0.193

Stage variable was log-transformed. Chl. *a* – multi-annual average of chlorophyll *a* concentration of stocked lakes in μg L^{-1}

(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 seven 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 four 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 km 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. Regression analysis testing for the effect of lake trophic status on fat content indicated that silvering stage was the only significant predictor of eel fat content, whereas chlorophyll *a* concentration was non-significant. All eels were collected in rivers outflowing of mesotrophic lakes, with narrow range in chlorophyll *a* concentrations. This might explain why no significant relationship between trophic status and fat content was detected, suggesting that our results apply 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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