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Occurrence of the European eel in lakes in the northern part of its distribution area is limited to low-altitude coastal areas, likely due to topographical conditions

Anders Foldvik*, Eva M. Ulvan, Eva B. Thorstad and Trygve Hesthagen

*Norwegian Institute for Nature Research, P.O. Box 5685, NO-7485 Trondheim, Norway (*corresponding author's e-mail: anders.foldvik@nina.no)*

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With the decline of the European eel, protection measures in all parts of the eel's distribution area may be increasingly important. Norway has a vast coastline (58°–71°N), but the distribution of eel has been largely unknown. We analysed data from questionnaires on fish distribution, covering 30 575 Norwegian lakes. Eels were recorded in 1773 lakes. The distribution was largely restricted to low altitude lakes in coastal areas (95% of the lakes with eels were situated below 295 m a.s.l., and within 87 kilometres from the sea). The occurrence of eels decreased towards the north, and only 5% of the lakes with eel were located north of 64.5°N. The northernmost lakes with eel were at 70.6°N, in the Barents Region. The degree to which man-made migration barriers restrict the distribution of the European eel in Norwegian freshwater should be further researched and data on the eel life history and densities are also largely missing.

Introduction

The European eel (*Anguilla anguilla*) is a panmictic species, with a common spawning area in the Sargasso Sea (Palm *et al*. 2009, Als *et al.* 2011). Eels undertake long migrations between the spawning and feeding areas. Their feeding areas extend to fresh, brackish and coastal waters in Europe, and African and Asian coasts of the Mediterranean and Black Sea (Tesch 2003, van Ginneken and Maes 2005). The major concentrations of eels have been reported in the Bay of Biscay and in the western Mediterranean, based on fishery yields (Dekker 2003). From the western Mediterranean and towards northern Europe, there seems to be a decline in eel densities (Dekker 2003). The northernmost observations of the European eel have been recorded in Finnmark, which is the northernmost county of Norway (Schmidt 1909, Bergersen and Klemetsen 1988, Davidsen *et al.* 2011). European eel has also been occasionally recorded in the Barents Region of Russia, on the Kola Peninsula (Davidsen *et al.* 2011).

The European eel has declined at least since the 1960s–1970s (Bornarel 2018, ICES 2018). In 2018, glass eel recruitment was at only 2% of the 1960–1979 level in the North Sea and 10% elsewhere (ICES 2018). The exact causes for the decline are not well understood, but several factors might have contributed, such as exploitation, pollution, migration barriers, hab-

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itat loss, changes in ocean conditions, introduced parasites and other anthropogenic factors (e.g. Dekker 2003, Geeraerts and Belpaire 2010, Durif *et al*. 2011, Kettle *et al*. 2011, Lefebre *et al.* 2013). Due to the decline, the European eel has been included as a critically endangered species in the Red List of Threatened Species by the International Union for Conservation of Nature (http://www.iucnredlist.org/details/60344/0).

With the decline of European eels and reduced habitat quality in many watersheds, it may be increasingly important to protect the eel in all parts of the distribution area. Knowledge of the distribution of species is an imperative foundation for sustainable management. In Norway, European eels inhabit both marine and freshwater areas (e.g. Durif *et al*. 2011, Larsen *et al*. 2015). The distribution of eels have been little studied and remains unclear, although there are large areas of potential eel habitats. Norway has a long coastline, covering 103 000 kilometres including islands, with a mainland stretching from 58° to 71°N (http://www.kartverket.no/Kunnskap/Fakta-om-Norge/). There are about 1300 watersheds with anadromous salmonids (http://www.miljodirektoratet.no/no/Tjenester-og-verktoy/Database/Lakseregisteret1/), and about 38 845 lakes larger than 0.04 km^2. The aim of this study was to map and characterize the distribution of the European eel in Norwegian lakes, using a large data set on the occurrence of different species of fish based on questionnaires answered by local people. We tested the null-hypotheses that the distribution of the European eel was not affected by elevation, lake size (surface area), latitude or distance from the sea. We also compared the distribution of the European eel with the distribution of the Atlantic salmon (*Salmo salar*), which is another diadromous species occurring in many Norwegian watersheds, and for which detailed distribution data are available.

Methods

Mapping the occurrence of the European eel in Norwegian lakes is based on questionnaire surveys that were mostly carried out from mid-1970 to mid-1990 (e.g. Hesthagen *et al*. 1999, Tammi *et al*. 2003). Later, such information has been collected in different regional projects carried out by the Norwegian Institute for Nature Research. In each municipality, we searched for people with good knowledge of the fish resources in lakes (Hesthagen *et al*. 1993). Such contacts included those employed by the local environmental management administration, fishery authorities, active members of local fishing associations and land owners. Each person was asked to answer the survey, either by postal inquires or by personal interviews. Information was obtained, if possible, from more than one person in cases of uncertainties. The main questions asked for each lake were: (1) the presence, also historically, of different species (presence/absent); (2) perceived status category or relative abundance of each species (abundant, normal, sparse or lost); (3) possible change in abundance over the last decades (no change, increased, decreased or lost); (4) the origin of each species (native or introduced); and (5) spawning conditions. Information regarding the European eel was restricted to data on presence/absence.

To identify factors that may affect the distribution of the European eel in Norway, we combined the information from these questionnaires with geographic data. Information on fish species occurrence from 30 575 lakes was included in the analysis, and 29 398 of these lakes were reported to contain fish. Information on the elevation, coordinates of lake centroids, lake area and distance from the sea were included in the analyses. Coordinates of lake centroids were used to extract elevation from the 10-m DEM (digital elevation model) and lake areas from the N50 map series (all map data from The Norwegian Mapping Authority). Distance from each lake to the sea was found by converting the 10-m DEM to a flow direction raster, which indicates the direction of the steepest drop from all raster cells. This was subsequently converted to a flow length raster, for each cell counting the number of downstream cells (using the Spatial Analyst Tools in ArcGIS 10.4), giving the distance from the lake to the sea along the rivers, “as the eel swims”. For lakes in catchments draining across the border to Sweden or Finland, the distances from the border to the sea were manually measured on an online map (kart.gulesider.no) using a fixed scale of approximately 1:100 000. This distance was then added to the distance from the lakes to the border.

Man-made migration barriers could affect the distribution of the European eel but were not included in the analyses because of the following issues: (1) we had no data to match the timing of eel recordings with the timing of the construction of the different dams; (2) we had no information on the characteristics of the dams to assess which of them are potential migration barriers to eels; and (3) we had no data on the exact distribution range of eels in the different watersheds to match with the exact location of the dams, since the data on the eel distribution are based on distribution in lakes and not in rivers.

The initial inspection of the variables (Fig. 1) revealed a significant correlation between elevation and distance from the sea ($R = 0.54$, $p \leq 2.2 \times 10^{-16}$), and between latitude and longitude ($R = 0.91$, $p = < 2.2 \times 10^{-16}$). Longitude was excluded from the analysis since latitude was a more relevant measure. This is because the Norwegian coastline has a large latitudinal variation, with a more logical causal link with the migration route of migrating fish such as the European eel. Both elevation and distance to the sea were included in the analyses.

A generalized linear model (GLM) with a logit canonical link function suitable for binomial data, with presence/absence of reports of the European eel as the response variable, was performed to test the null-hypotheses that the distribution of the European eel was not shaped by elevation, lake size (surface area), latitude or distance from the sea. The full model consisted of the north coordinate of the lake (UTM33), elevation (m a.s.l.), distance from the sea (m), lake area (km^2) and an interaction term between distance from the sea and elevation. This interaction was included because the combined effect of altitude and distance in terms of gradient could affect the eel distribution. Model selection was performed by removing the least significant variables until none could be removed without causing significant ($p > 0.05$) increase in model deviance (χ^2-test). All analyses were conducted in R ver. 3.4.3 (R Core Development Team 2016) using Rstudio (ver. 1.1.383).

The distribution of the European eel was compared with the distribution of another diadromous species, the Atlantic salmon, for which there are detailed distribution data (collected from the Norwegian Environment Agency database). Distribution data for the Atlantic salmon were imported to ArcGIS, and presence/absence of the European eel in catchments with the Atlantic salmon was found. For the catchments with both the European eel and the Atlantic salmon, distances between the topmost reach of the Atlantic salmon and the European eel were found using the same distance raster as above.

Results

Of the 30 575 lakes included in this study, the occurrence of European eel was reported for 1773 lakes, covering a total surface area of 1990 km^2, mainly located in southern and central Norway (Fig. 2a). These lakes belonged to 141 of Norway's 260 hydrogeographic regions, that include the catchment areas of all small and large catchments that drain into the sea within a costal section (https://www.nve.no/karttjenester/kartverktoy/nve-atlas/). European eel distribution was largely restricted to low altitude lakes, as 95% of the lakes with reported occurrence were located below 295 m a.s.l. (Fig. 3a). The median altitude of lakes with European eels was 69 m a.s.l., and 50% of them were located between 25 and 165 m a.s.l. The lakes with eel were situated at lower altitudes than the lakes where eels were reported as absent (Fig. 3b).

Lakes with European eels were also mainly located close to the sea, as 95% of the lakes with reported occurrence were closer to the sea than 87 km (Fig. 3c). The median distance from the sea of the lakes with eels was 7.1 km, and 50% of them were located between 2.3 km and 20 km from the sea. Eels were recorded in four lakes within the catchment of the river Trysilelva (Fig. 2a circle), which flows eastwards into Sweden. The distance of the uppermost lake from the sea is 669 km, and it is the longest distance from the sea where European eels were reported. Most lakes with eels (95%) had a surface area smaller than 3.4 km^2 (median = 0.14 km^2, and 50% of the lakes were in the range 0.06–0.42 km^2). Lakes with European eels were larger than those without eels (Fig. 3d and e).

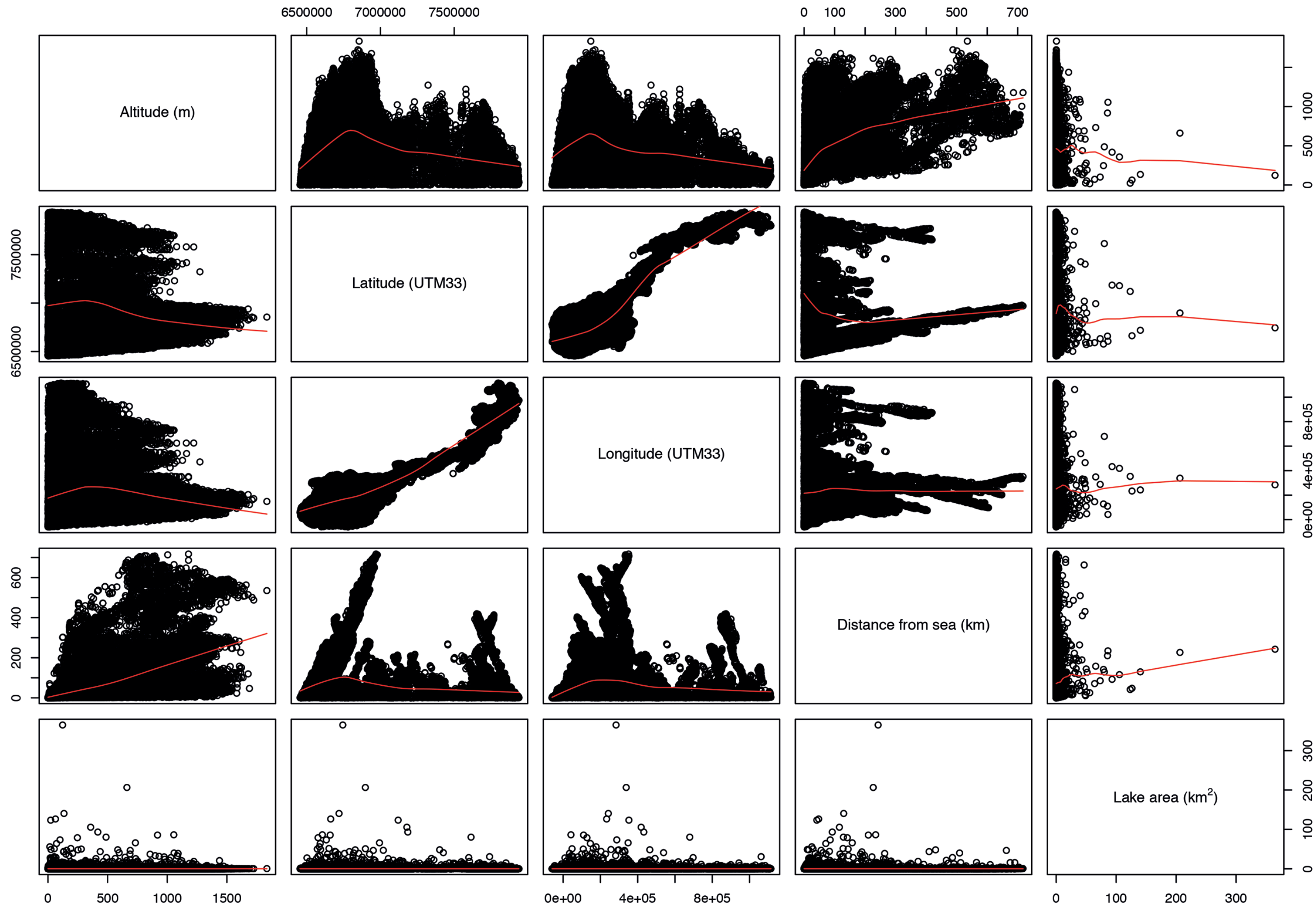

Fig. 1. Attributes of the lakes (*n* = 30 575) included in the binominal generalized linear model plotted against each other. Lines indicate relationships between variables using the LOWESS smoother.

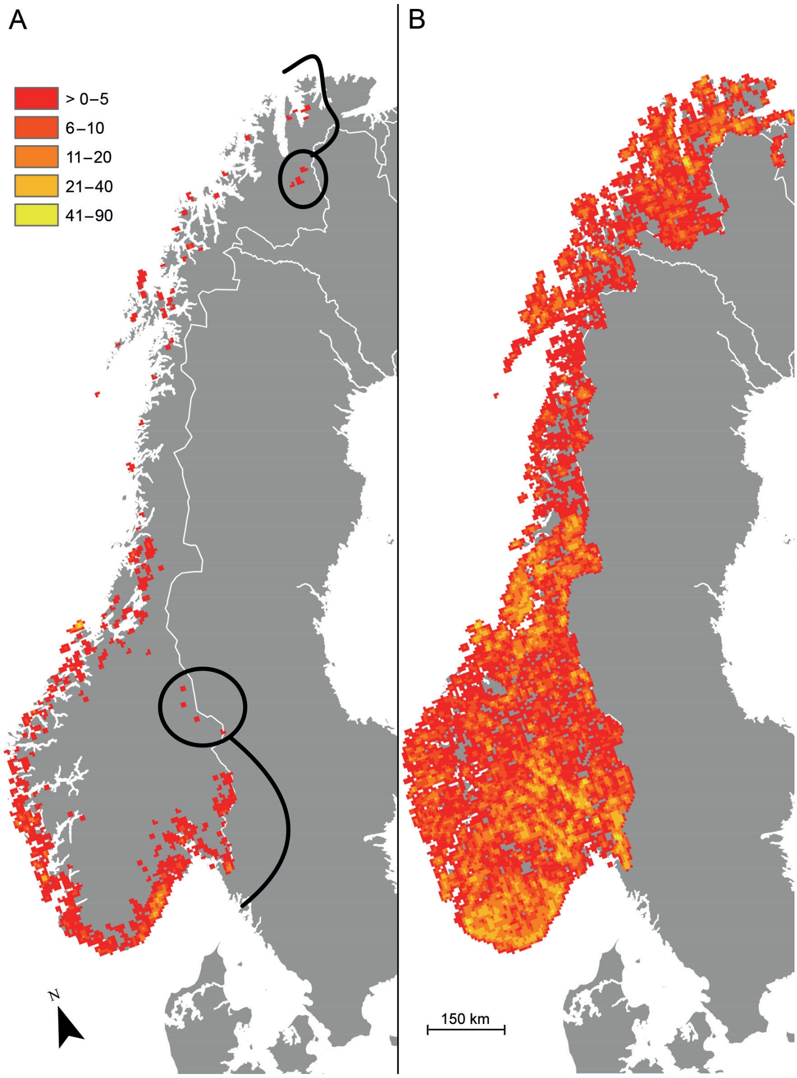

Fig. 2. Maps of Norway showing (**a**) point density of lakes with reported occurrence of eels, and (**b**) point density of all lakes in the study with reports of fish species occurrence. Colours from red to yellow indicate low to high number of points within circular areas with 5-km radius. For locations enclosed in black circles, migration route from the sea is indicated by black lines.

Model selection on the full binominal generalized linear model with the presence/absence of reported eel as the response showed that the interaction between altitude and distance from the sea could be removed ($p = 0.09$). The main effect of the latter variable could then also be removed ($p = 0.07$). No further variables could be removed and consequently the final model consisted of latitude, altitude and lake area (Table 1). The deviance of the final model (8269.7) was smaller than the critical values of the χ^2 distribution (95%, df = 30 571) equalling 30 978.86, indicating that overdispersion was not present. The analysis showed that the likelihood of lakes containing the European eel decreased with both latitude and altitude and increased with lake area. Even though lakes towards the north had a decreased likelihood of containing eels, the distribution area continued to the northernmost areas of the country. European eel was reported to occur in the Tana watercourse in Finnmark County. This means that eels must have passed the sea area further north than northernmost point of mainland Europe, which is Cape Nordkinn in Norway at 71°8´N.

The occurrence of European eels were reported in 111 of the 446 Norwegian watersheds holding Atlantic salmon. In 73 of these 111 watersheds (66%), eels were reported in

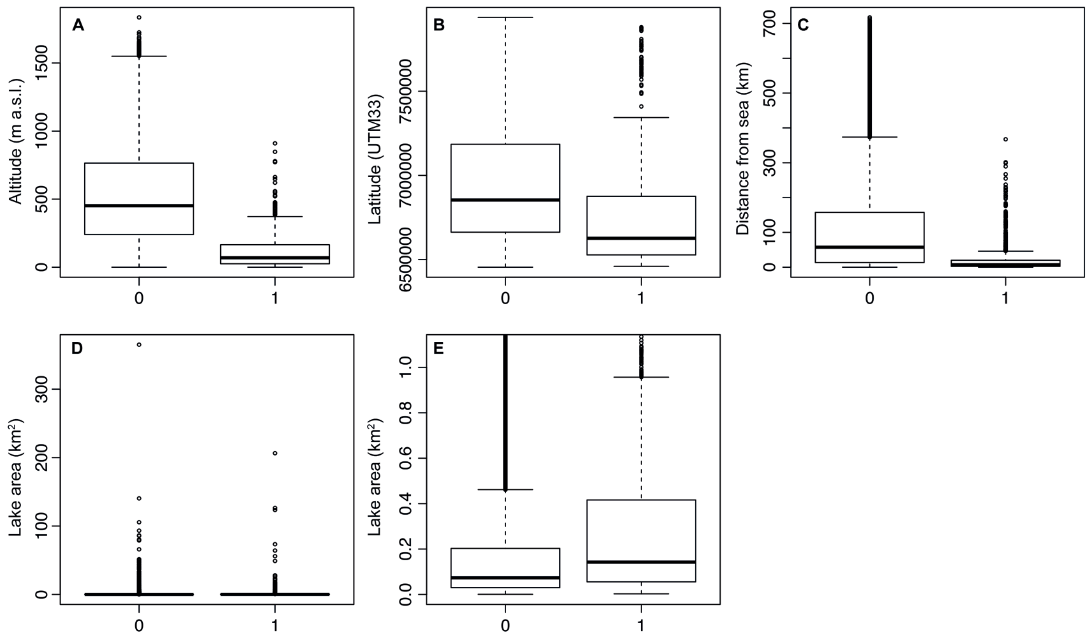

Fig. 3. Boxplots of (**a**) altitudes (m a.s.l.) of lakes with eels (1, n = 1773) and without eels (0, n = 28 802), (**b**) latitudes (UTM33) of lakes with eels (1, n = 1773) and without eels (0, n = 28 802), (**c**) distance from sea in kilometres for lakes with eels (1, n = 1773) and without eels (0, n = 28 802), (**d**) size of lakes in square kilometres of lakes with eels (1, n = 1773) and without eels (0, n = 28 802), and (**e**) same as in **d** but only lakes < 1.1 km^2. Lines within boxes indicate medians; boxes indicate the 25th and 75th percentiles, respectively; whiskers indicate the most extreme data points within 1.5 times the interquartile range and dots are observations outside this range.

lakes upstream of the stretch that is accessible to Atlantic salmon. Where eels were reported upstream of Atlantic salmon, the most upstream lakes with reported occurrences of eels were 13.1 km (median) from the stretch accessible to Atlantic salmon (mean ± SD = 22.1 ± 31.85 km, range = 0.53–223.50 km).

Discussion

In this study, the occurrence of the European eel was assessed in 30 575 Norwegian lakes. Eels were reported to occur in 1773 of these; mainly in low altitude lakes near the coast. Altitude and distance from the sea were highly correlated, but altitude was more important in explaining the distribution of European eels than the distance from the sea. The fact that European eels were reported in lakes farther inland in some watersheds and the importance of altitude in the model, suggest that the European eel is not restricted by migration distance upstream *per se*. Ibbotson *et al*. (2002) described the freshwater migration of the eel as mainly being a simple diffusive process, which will also result in a decline

Table 1. Summary of the binominal generalized linear model that best accounted for reported presence/absence eels in 30 575 Norwegian lakes. Null deviance: 13 538.4 on 30 574 degrees of freedom. Residual deviance: 8269.7 on 30 571 degrees of freedom.

Parameters	Coefficients (SE)	z	p
Intercept	14.68 (0.57)	26.35	$< 2 \times 10^{-16}$
Altitude (m)	-0.011 (2.71×10^{-4})	–40.12	$< 2 \times 10^{-16}$
Latitude (UTM33)	-2.18×10^{-6} (8.14×10^{-8})	–26.76	$< 2 \times 10^{-16}$
Lake area (km^2)	0.028 (6.81×10^{-3})	4.11	3.91×10^{-5}

in the number of eels with distance from the coast. Regardless of migration being diffusive or directional, eel distribution is likely to be associated with the chance of encountering a migration barrier, preventing them from further upstream passage. Eels are known to inhabit similar environments as other freshwater fish species, and in areas that provide enough food, such as lakes, fast and slow flowing river stretches, ditches and marshland (e.g. Deelder 1984, Laffaille *et al*. 2003, Domingos *et al*. 2006, Westerberg and Sjöberg 2015). It is therefore reasonable to believe that the distribution of the European eel in freshwater, to a large degree, depends on how far they can move upstream in watersheds before they are hindered by an impassable barrier. The coastal distribution pattern of lakes with eels, as shown in this study, is probably not due to a skewed distribution of lakes included in the survey, because many lakes distributed throughout the country were included.

The distribution of the European eel in Norway coincides to some extent with that of the Atlantic salmon, which is another diadromous species distributed in watersheds along the entire coastline. The Atlantic salmon also has a coastal distribution because they are limited by impassable migration barriers usually from a few to tens of kilometres from the sea (Anon. 2017). However, the fact that European eels were reported farther upstream than Atlantic salmon in 66% of the watersheds where both species were recorded, indicates that eels can sometimes cross migration barriers impassable to Atlantic salmon. However, eels were not reported much farther upstream in these watersheds (median 13 km). Unlike Atlantic salmon, eels can climb vertical, wet walls (Knights and White 1998), and can move short distances on wet substrate on land (Ellerby *et al*. 2001). Eel individuals may take several years to move upstream in a watershed and a maximum migration rates of 8 to 46 km per year in many watersheds have been reported (Aprahamian 1988, Mann and Blackburn 1991). Hence, the age and size distribution of the eel change towards older and larger specimens farther upstream in a watershed (Aprahamian 1988, Mann and Blackburn 1991). Eels climb vertical walls better when they are smaller than approximately 12 cm in body length; these smaller-sized eels adhere to walls easier when they climb compared with larger-sized eels (Knights and White 1998). This implies that a migration barrier that may be passable for small European eels, but impassable for larger specimens, may be crucial in determining their range within a watershed. Eels may also use smaller creeks and ponds not suitable for Atlantic salmon. Thus, eels may move further upstream in tributaries than Atlantic salmon.

Some migration barriers may be passable for the Atlantic salmon but not for the European eel because eels cannot jump and they may also be poorer swimmers against strong flow (McCleave 1980, Knights and White 1998, Porcher 2002). However, we do not know if this explains why the European eel potentially has a more restricted distribution than the Atlantic salmon in some watersheds. With our data, we can only demonstrate, with certainty, cases where eels are further distributed upstream than salmon, not the opposite. This is because we have data on the full distribution range in lakes and rivers for the Atlantic salmon; whereas for the European eel, we have only lake data and do not know how far upstream they may migrate along the rivers from these lakes.

From our results, European eels were distributed from the southernmost to the northernmost areas of Norway. To reach the northernmost lakes, eels must pass the northernmost point of mainland Europe at 71°8′N. This is in accordance with previous observation of the European eel on the Russian Kola Peninsula (Davidsen *et al*. 2011). Previous studies have reported low densities of eels at the northernmost parts of the country (Bergersen and Klemetsen 1988, Davidsen *et al*. 2011). Our study did not provide information on eel density — only on the presence or absence, but our results showed that lakes towards the north have a decreased likelihood of containing European eels. This is likely due to European eel distribution being skewed towards southern regions. However, the occurrence of eels in northern Norway may also, to some extent, be underestimated due to fewer lakes being included in the survey.

Latitude may affect the distribution of eels through several mechanisms. It could be a consequence of where juvenile eels encounter the coast due to the Golf Stream pattern (Durif *et al*. 2011). However, knowledge on how the active and passive components of the migration of juvenile eels shape their distribution is limited (van Ginneken and Maes 2005). It could also be a consequence of preferred climatic conditions or because the productivity of lakes decreases towards the north. The European eel is a facultative catadromous species and some individuals never enter fresh water during their entire life cycle (Arai *et al*. 2006, Daverat *et al*. 2006). The tendency for eels to enter fresh water might decrease towards northern Norway (Daverat *et al*. 2006) because of the relative difference in productivity changes with latitude — with productivity favouring towards remaining in salt water in northern areas (Gross *et al*. 1988, Tsukamoto *et al*. 1998). European eels, therefore, experience habitats with relatively higher productivity in salt water than in fresh water towards the north. Experimental fisheries in the sea around 65°29N in 1958 indicated a sufficient amount of European eel to support fisheries, but the possibility of delivering eel to the buyer's market were limited (Halaas 1958). Hence, the eel density may decrease relatively more towards the north in freshwater lakes than in the sea, but this has, to our knowledge, not been studied. Climate change has the potential to change the suitability of both saltwater and freshwater habitats for the European eel. For freshwater habitats in Norway, climate change has been predicted to result in a severe increase in organic carbon (Larsen *et al*. 2011), possibly reducing fish productivity via light limitation (Karlsson *et al*. 2009). On the other hand, increased water temperatures in fresh water in the north may be favourable for eel because of a longer growth season.

The distribution of European eel as reported here is likely an underestimate of their occurrence. There are about 446 watersheds with Atlantic salmon in Norway, but only 111 of them have lakes with reports of eel. Since European eel is distributed along the entire coastline and live in a large variety of freshwater habitats, it is likely that they occur in most watersheds with anadromous salmonids in Norway (compare with Larsen *et al.* 2015). Since this study is based on eel occurrence in lakes, watersheds that do not contain lakes in the lower parts accessible for diadromous fish were not included. With Norway having approximately 1300 watersheds with anadromous populations of brown trout (*Salmo trutta*) and/or Arctic char (*Salvelinus alpinus*), the underestimation of eel occurrence is likely to be large. This is especially the case in areas with small lakes having none or few such targeted fish species; and hence, a low fishing burden.

Data on the occurrence of the European eel by means of questionnaires have obvious shortcomings. However, this is the only method for obtaining such information from a large number of lakes. In Norway, there is generally good knowledge about lentic fish stocks; there is a long tradition and keen interest in exploiting them and all citizens are allowed to fish in most lakes. For many localities, this also involves gillnet fishing, where brown trout and Arctic char are the target species. However, regional differences in knowledge about European eels may affect the outcome of the analysis. The European eel has, to a limited extent, been a targeted fish species in lakes in Norway. Reports of its occurrence are therefore mainly based on the observation of mucus in gillnets and occasional rod catches. Thus, local knowledge of their occurrence is more limited than of species such as brown trout and Arctic char. There has also traditionally been little interest in consuming European eel in Norway, and the catches have mainly been limited to areas where they could be delivered for export, although there are some exceptions (e.g. Huitfeldt-Kaas 1904, Halaas 1953, Jensen 1972, Kristensen 1980). Eel fishing mainly took place in southern and southwestern Norway, but also to some extent in central Norway, before the total ban of eel fisheries in 2010 (ICES 2017). These may therefore be the areas with the best local knowledge on the occurrence of the European eel.

The distribution of the European eel may be restricted by man-made barriers, such as power station dams in rivers (e.g. Knights and White 1998). An analysis of man-made barriers is not included in this study due to limitations from the data, as described in the Methods section. However, the main conclusions of this study are still valid. The coastal and low-altitude distribution of lakes with eels remain consistent in the data set, even with many watersheds without man-made barriers also included in the study. Further, the decrease in the occurrence of eels towards the north cannot be explained by the presence of man-made migration barriers, because there are fewer man-made barriers in the north than the south. Barriers like power station dams vary largely in their characteristics, and to which extent they may act as barriers to upstream migrating eels. Many of the dams registered in the Norwegian database seem not to hinder upstream migration because for a subset of data where we have both information on eel distribution in lakes and dams (132 watersheds), at least 63% of the watersheds had the occurrence of eel upstream of the dams (authors' own data). This is a minimum estimate because we lack the exact distribution range of eels, since this is based on data from lakes and not from rivers. Even though many dams may hinder upstream migration of eels, this may not largely impact the main pattern of eel distribution in Norway, as analysed in this study. This might happen if many of the low elevation dams are passable for eels, whereas the dams not passable may be situated near high waterfalls, where eel would be unable to pass. However, passable dams may still reduce the number of eel swimming to upstream areas, although they do not fully hinder the upstream migration.

Glass eel fishing has always been prohibited in Norway (ICES 2017) and there has not been any tradition for restocking of glass eel or elvers (e.g., Huitfeldt-Kaas 1904, Halaas 1953, Kristensen 1980). Hence, the distribution of eel recorded in this study is to our knowledge not extended in comparison with the natural distribution due to restocking. There may be one exception — eel reports from four lakes in the catchment of the river Trysilelva, located about 670 km from the sea. The river Trysilelva drains eastwards into Sweden (named Klarälven in Sweden), to Vänern, and finally as the river Göta älv into the Kattegat Sea at Gothenburg. There have been releases of eel in the Swedish Lake Vänern since about the year 1900. These were eel that had entered the watershed naturally, but were captured in Göta älv at Trollhättan for assisted transport past dams and hydropower stations. Later, there have been releases of European eels of both local origin and imported from France and the United Kingdom in several parts of the watershed in Sweden (H. Wickström, SLU, pers. comm.). Hence, the origin and migration distance of eels in lakes in this watershed in Norway is not known because they might have originated from releases in Vänern or from releases in areas closer to Norway.

In conclusion, this study shows that the European eel is distributed in watersheds along the entire Norwegian coastline, although with a reduced occurrence towards the north, and with the main distribution in low-altitude lakes near the sea. Other studies have shown that part of the population also resides in marine areas along the Norwegian coast. The European eel in Norway has declined over the past decades as in other parts of Europe (Durif *et al*. 2011, Bornarel *et al*. 2018, ICES 2018, Poole *et al*. 2018). This was especially the case in south and southwestern Norway where eels, in addition to a general decline in spawning, were negatively impacted by poor water quality due to acidification (Larsen *et al*. 2015). However, the European eel has recovered in formerly acidified rivers as a result of liming (Larsen *et al*. 2015) and the distribution of eels in this area is probably no longer impacted by acidification. The degree to which natural and man-made migration barriers restrict the distribution of eels in Norwegian freshwater should be further researched and data on the life history and densities in fresh water and the sea are largely missing.

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