

Habitat use and growth of yellow-stage European eel in coastal and freshwater ecosystems in Norway

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Abstract

Many anguillid eel species display facultative catadromy. Some eel spend their entire life cycle in marine coastal areas, but the geographical extent of this, especially at the extremes of their distributional ranges, is unknown. We analysed otolith Sr:Ca and Ba:Ca from yellow-stage European eel (*Anguilla anguilla*) sampled along the coast of Norway and in several freshwater lakes (58°N–63°N), to infer their initial settlement and later life movement patterns with regards to habitat salinity. Most eel (80%) sampled in marine habitats ($n = 371$) had settled and remained in marine water, but 20% had moved between marine and freshwater habitats and were hence classified as inter-habitat shifters. Among freshwater sampled eel ($n = 99$), 80% had settled and remained in fresh water, but 20% were classified as inter-habitat shifters. The average growth rates for marine water residents, inter-habitat shifters, and freshwater residents were 35, 27, and 17 mm·year⁻¹, respectively. Northern European shallow marine habitats may serve as important yellow eel growth habitats and may be critical to buffer the European eel population against the general decrease in continental recruitment.

Key words: otolith microchemistry, anguillids, *Anguilla anguilla*, salinity, age, growth rate

1. Introduction

The decline of the panmictic European eel (*Anguilla anguilla*) population is well documented (Drouineau et al. 2018; ICES 2020). The data used to support this apparent decline have mostly been based on eel collected in freshwater ecosystems. This is probably because the European eel was, for a long time, regarded as a classic catadromous species (i.e., all eel recruit to fresh water after being spawned in marine waters), and because it is much easier to conduct surveys for eel in freshwater habitats. All northern temperate zone (i.e., *A. anguilla*, *Anguilla japonica*, and *Anguilla rostrata*) and many tropical anguillid eel species (e.g., *Anguilla australis* and *Anguilla dieffenbachia*) are now considered to be facultatively catadromous, and are highly plastic in their habitat use (Jessop et al. 2002; Arai et al. 2004; Kotake et al. 2005; Daverat et al. 2006). Three general patterns of habitat use were identified: freshwater residents (i.e., true catadromous eel), marine water residents (here, eel that reside in salt-water for the entire continental growth period), and inter-habitat shifters (here, eel that move between freshwater and marine habitats). The fact that northern temperate eel are facultatively catadromous has only recently been confirmed (Tsukamoto et al. 1998; Lamson et al. 2006), but observations on eel that reside in marine water and move between

habitats date further back (Bertin 1956; references in Dekker 2019).

European eel are semelparous and migrate to the Sargasso Sea to spawn (Schmidt and Regan 1923; Tesch 2003). Eel larvae (leptocephali) drift with the Gulf Stream towards North Africa and Europe. They metamorphose into glass eel when they reach the continental shelf, and then migrate to coastal areas and become yellow eel as they settle in continental marine or freshwater habitats. The continental growth phase, or yellow eel stage, lasts from 5 to 30 or more years (Poole and Reynolds 1996; Durif et al. 2020), after which they become silver eel and migrate back to the Sargasso Sea to spawn.

There is much less knowledge about eel in marine coastal waters compared to those in freshwater habitats (ICES 2018). Notably, the abundance and distribution of eel in marine waters is poorly known (Righton et al. 2021). It has been suggested that the population decline in eel has been steeper in freshwater compared to marine habitats (Edeline 2007), and that it is primarily marine eel that contribute to future recruitment (Tsukamoto et al. 1998).

Marine resident eel and inter-habitat shifters seem to be present in many areas within the species' distributional range, but their proportion varies depending on the location. They are present in Mediterranean lagoons and have been

identified in estuaries in southwestern France (Daverat and Tomás 2006; Capoccioni et al. 2013), and also in the Baltic Sea (Limburg et al. 2003; Shiao et al. 2006; Lin et al. 2012; Sjöberg et al. 2017). Marine water residents dominate along the coast of Ireland (Arai et al. 2019). Based on the difference in food abundance between marine and freshwater habitats (Gross 1987), marine residency of temperate zone anguillid eel should occur more frequently at high latitudes where freshwater productivity may be lower compared to that of adjacent coastal regions (Tsukamoto and Arai 2001). This might be particularly true for European eel along the coast of Norway because of the more favorable coastal environmental conditions (Jessop et al. 2004). However, little is known about the pattern of habitat use by European eel from the North and Norwegian Seas (Andersson et al. 2019).

In Norway, the European eel is common along the country's entire latitudinal range (i.e., 57°N–71°N; Foldvik et al. 2019), and across a variety of marine and freshwater habitats (Thorstad et al. 2010; Durif and Skiftesvik 2019). There used to be a commercial marine fishery, at least at latitudes below 60°N (Durif and Skiftesvik 2019), but the proportion of Norwegian eel utilizing freshwater or marine habitats are unknown. As both the commercial and recreational fishing for eel have been under a moratorium since 2010 (although limited scientific fishing is still allowed), most Norwegian coastal and freshwater habitats are free of targeted eel fishing pressure and, therefore, offer a unique setting to study the natural habitat use of this species.

Otolith microchemistry is used routinely to study the migration and movement patterns of teleost fishes (Walther and Limburg 2012; Walther 2019). The method has been applied extensively in studies on temperate and tropical anguillid eel, where it has revealed that catadromy is not obligatory (e.g., Tsukamoto et al. 1998; Lamson et al. 2006; Chino and Arai 2010). The method is based on the assumption that certain trace elements, such as strontium and barium, are incorporated into otoliths in proportion to their environmental availability (Campana 1999). Thus, if differences in water chemistry exist, for instance between fresh- and marine water, and if fish move between these water bodies, then these differences can be identified in their otoliths. The time recording property of otoliths (i.e., the presence of incremental growth rings) can be used to extract a retrospective chemical habitat use profile from otoliths. This chemical history can, in turn, be interpreted in the context of movement and habitat use patterns through time. The prevalent chemical marker used in eel otolith microchemistry studies is the strontium to calcium ratio (Sr:Ca) (e.g., Tsukamoto et al. 1998; Arai et al. 2019), which usually displays a positive relationship with salinities up to 20 PSU (Tabouret et al. 2010). Complementary use of Sr:Ca and the barium to calcium ratio (Ba:Ca) (which is inversely related to salinity) could be valuable, but are less common (Tabouret et al. 2010; Daverat et al. 2011; Rohtla et al. 2021), because Ba has a nutrient-like profile in the water column (Coffey et al. 1997) and its application is, therefore, less straightforward in estuarine areas (Jessop et al. 2012).

The main objective of this study was to determine the distribution and relative occurrence of the three main eel habi-

tat use patterns in Norwegian coastal and inland waters using otolith Sr:Ca and Ba:Ca ratios. Specific aims were to study (i) whether initial settlement as a glass eel occurred in marine or freshwater habitats and (ii) if and to what extent eel shifted habitat later in life. This knowledge will help clarify the role of marine water habitats during the continental growth phase of European eel in this region and, thus, contribute to more informed stock assessment and management actions. Our secondary objective was to estimate eel age and growth rates and to couple those data with otolith microchemistry to support a more complete understanding of eel general biology.

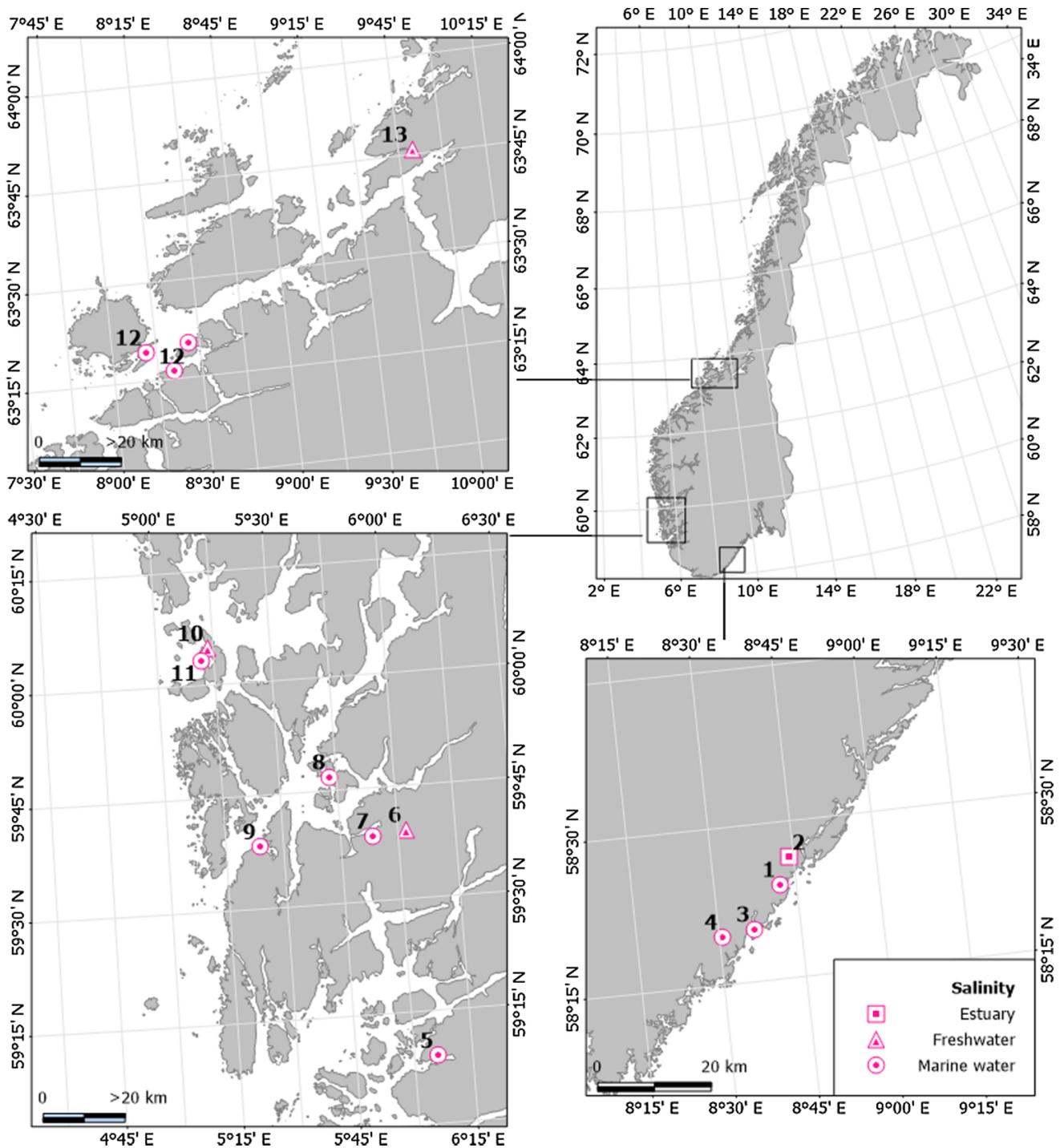
2. Materials and methods

2.1. Fish sampling and description of the study sites

Yellow eel were collected from various locations along the coast and in freshwater habitats in Norway (Fig. 1; Table 1). Eel were either obtained from authorized local fishers or caught by the coauthors. Fyke nets (mesh size at the cod end was ~8 mm, knot-to-knot, and 11 mm along the diagonal) and eel pots (mesh size was ~10 mm, knot-to-knot, and 15 mm diagonal) deployed at depths of 1–8 m were used to collect the eel. All eel were euthanized with an overdose of clove oil. Total length and wet mass were measured for all eel. To assure that only yellow eel were included to the final sample, the silvering stage was determined following Durif et al. (2005). All eel, except two, were females. The study was approved by the Norwegian Animal Research Authority and performed in accordance with animal welfare regulations (FOTS ID 15952).

All marine water sampling sites are characterized by salinity and temperature stratification, which is typical for the Norwegian coast. In the Arendal area, located on the Norwegian Skagerrak coast, eel were sampled from four sites: outer and inner coast, Nidelva River mouth area in the sea (all combined to one Arendal sample; salinity poly- and euhaline) and Hølen, which is considered a fjord with strong freshwater input from the Nidelva River (salinity oligo- to polyhaline). Because of the dynamic, estuary-like, salinity regime, the Hølen sampling area is considered to be part of the Nidelva Estuary. In the Grimstad region, located on the Norwegian Skagerrak coast, eel were sampled from two sites: outer coast and Landvikvannet. Sampling at the outer coast was carried out in the Grosfjord, where the water is polyhaline and low in oxygen (Vann-nett; <https://www.vann-nett.no>). Landvikvannet is an inland brackish water lake (1.85 km², average depth = 10 m, and maximum depth = 25 m), where the upper layer has low salinity (<15 PSU) and is rich in oxygen, but under 10 m salinity is ~20–25 PSU and conditions are anoxic (Eggers et al. 2014). This lake is connected to the ocean by a 3 km long canal (1–4 m deep) constructed in 1877. Small freshwater streams empty into the lake while saltwater flows in, depending on the tide. Etnesfjord, Fisterfjord, Hardangerfjord, Bømlofjord, Austevoll, and Smøla are all categorised as euhaline, but variable number of freshwater streams empty into

Fig. 1. The study area and sampling locations in Norway. Sampling location numbers correspond to those in Table 1.



these regions (Vann-nett; <https://www.vann-nett.no>; van der Meeren et al. 2021).

Lake Litledalsvatn is a freshwater lake (0.95 km²), located ~8 km from the mouth of the Etne River in the Etnefjord. Lake Fiskevatn (Austevoll) is a freshwater lake (0.08 km²), located ~200 m from the sea. River Botnelva is a 10.2 km long river, located ~6 km from the sea, and is connected to Bjugn-fjord through two lakes and streams.

2.2. Otolith preparation and chemical analysis

Sagittal otoliths were extracted from each fish shortly after their capture or sometime later in the laboratory after thawing frozen samples. Otoliths were cleaned individually using tissue paper and stored dry in plastic vials. For chemical analysis, one randomly chosen otolith per individual was embedded in epoxy resin (Struers Epofix; Struers, Westlake, Cleveland, OH, USA). Each epoxy block was then manually

Table 1. Sampling locations (ID # referred to in Fig. 1), biological parameters measured, assigned habitat use pattern, number of eel sampled at each location (n), total body length (TL, mean \pm SD), and body mass (M , mean \pm SD) for European eel (*Anguilla anguilla*) collected from different marine (MW) and freshwater (FW) habitats in Norway.

ID	Location	Habitat	Latitude (°N)	TL (mm)	M (g)	n	Marine water resident (%)	Inter-habitat shifter (%)	Freshwater resident (%)
1	Arendal	MW	58.4	570 \pm 110	320 \pm 200	80	97	3	0
2	Nidelva Estuary	FW/MW	58.4	560 \pm 100	330 \pm 180	30	23	77	0
3	Grosfjord	MW	58.3	658 \pm 112	498 \pm 276	25	84	16	0
4	Landvikvannet	MW	58.3	614 \pm 91	390 \pm 215	24	100	0	0
5	Fisterfjord	MW	59.2	540 \pm 30	250 \pm 50	36	64	36	0
6	Litledalsvatn	FW	59.6	530 \pm 90	280 \pm 200	30	0	30	70
7	Etnefjord	MW	59.6	500 \pm 70	240 \pm 120	40	97	3	0
8	Hardangerfjord	MW	59.6	690 \pm 70	540 \pm 170	42	79	21	0
9	Bømlofjord	MW	59.8	530 \pm 70	260 \pm 140	31	87	13	0
10	Fiskevatn	FW	60.0	410 \pm 90	140 \pm 140	44	0	2	98
11	Austevoll	MW	60.0	490 \pm 70	200 \pm 82	33	79	21	0
12	Smøla	MW	63.3	530 \pm 70	330 \pm 150	30	57	43	0
13	Botnelva	FW	63.7	340 \pm 60	70 \pm 30	25	0	36	64
Total						470	62	21	17

ground on a grinding machine (Metaserv 250; Buehler Ltd., Lake Bluff, IL, USA) with silicon carbide impregnated sandpaper (using P400 and P1200 grit sizes; Buehler Ltd., Lake Bluff, IL, USA) until the core on the transversal otolith section was visible. Final polish was obtained using P4000 grit sandpaper. Individual otolith thin sections were then glued onto standard glass microscopy slides and stored in clean plastic containers for later analysis. Before the chemical analyses, all otolith thin sections were ultrasonically cleaned for 15 min in ultrapure water and subsequently dried in a laminar flow hood. Otolith thin sections were analysed for ^{24}Mg , ^{43}Ca , ^{88}Sr , and ^{137}Ba using laser ablation inductively coupled plasma mass spectrometry at the University of Tartu (Department of Geology). A continuous line scan was traced from the core to the edge (Fig. 2) in all samples using a translation rate (laser speed) of $5 \mu\text{m}\cdot\text{s}^{-1}$ and beam size (laser beam diameter) of $40 \mu\text{m}$ (also refer to the online Supplementary material, Table S1). A $40 \mu\text{m}$ beam size corresponds to $\sim 2\text{--}4$ months of eel life in fast growth periods, but this could decrease to a full year in slow growth periods. A reference glass material (NIST 612) and calcium carbonate standard (MACS-3) were analysed before and after every 15 otoliths. Data reduction to element:Ca in $\text{mmol}\cdot\text{mol}^{-1}$ is fully described in Rohtla et al. (2014). The average precision (%RSD) of ^{43}Ca , ^{88}Sr , and ^{137}Ba signals from NIST 612 during all analysis days was 22%. The average precisions for standardized Sr:Ca and Ba:Ca ratios were 0.7% and 1.2%; otolith Sr:Ca and Ba:Ca values were corrected for this drift. Occasional extreme outliers and random noise were removed from the dataset if the specific data point was larger than 1.5 times the median of the preceding and the following data point, and replaced by the median of the two points. A five-point running median followed by five-point running average was used to smooth the data further for visualization (modified from Sinclair et al. 1998). All prepared otolith thin sections were first inspected visually to detect vateritic regions as these represent an unstable form of

calcium carbonate and do not reflect the environmental history experienced by the fish (Tzeng et al. 2007). In one eel, one of the otoliths was entirely vateritic, so the second one was prepared and analysed. Otolith Mg:Ca was used as an additional tool to detect vateritic regions that were missed visually (Tzeng et al. 2007). Two eel with partially vateritic otoliths were removed from further analysis.



2.3. Water sampling and chemical analysis

Surface water samples were collected from eight freshwater sites to characterize the general chemistry in the study region and to corroborate otolith chemistry data. We did not

sample water at marine sites (where most of the eels were collected) because there is limited variation in seawater Sr:Ca and Ba:Ca. Both eels and water sample were collected at two sites (Fiskevatn and Litledalsvatn). Only water samples were collected at other freshwater sites. Water samples were collected with a syringe and filtered through 45 μm nylon filter into sterile sampling containers. To fix the samples, 2 mL of 5% HNO_3 was added to every sample after the filtration. All samples were refrigerated until analysis.

Water samples were analysed at the University of Tartu (Department of Geology) with Agilent 8800 QQQ ICP-MS. National Institute of Standards and Technology (NIST) water standard 1643f was used for precision and accuracy assessment. ^{43}Ca , ^{88}Sr , and ^{137}Ba were quantified and subsequently used to calculate Sr:Ca and Ba:Ca molar ratios for each site.

2.4. Age and growth rate estimation

Eel age and growth rate were determined to complement the otolith chemistry results. After the chemical analysis, otoliths were repolished, etched, and stained with toluidine blue or neutral red solution following standard procedures (ICES 2009, 2011). Mean annual growth rate was calculated by dividing the total length (mm) of the eel minus 70 mm, which is the mean size of glass eel when they recruit to European coasts (Elie 1979; Svedäng et al. 1996), by the continental age (years). Age and growth rate were then compared among locations, habitats and habitat use patterns. Age was also coupled to the otolith elemental profiles to determine the timing of inter-habitat shifting movements.

2.5. Data analysis and interpretation

To distinguish between marine and freshwater habitat use, otolith Sr:Ca and Ba:Ca reference values were established for fresh water using the eel sampled in freshwater habitats (i.e., Litledalsvatn, Fiskevatn and Botnelva). Mean otolith edge (ca. 100 μm) Sr:Ca and Ba:Ca values were calculated per each eel caught in fresh water. As unexpectedly high Sr:Ca values for fresh water were identified in the otoliths of eel from Fiskevatn (see Results; Fig. 3h), they were subsequently treated separately. The freshwater reference values for Litledalsvatn and Botnelva were calculated as mean of individual mean otolith edge values plus 2 times the standard deviation (SD) for the upper limit of Sr:Ca freshwater reference value (0.97 $\text{mmol}\cdot\text{mol}^{-1}$) and as mean of individual mean edge values minus 1 SD for the lower limit of Ba:Ca freshwater reference value (0.0014 $\text{mmol}\cdot\text{mol}^{-1}$). Only 1 SD was applied to Ba:Ca data because of less variation in reference values compared to Sr:Ca data. The freshwater reference values for Fiskevatn were calculated as mean of individual mean edge values minus 2 SD for the lower limit of Sr:Ca reference value (1.14 $\text{mmol}\cdot\text{mol}^{-1}$) and as mean of individual mean edge values minus 1 SD for the lower limit of Ba:Ca freshwater reference value (0.005 $\text{mmol}\cdot\text{mol}^{-1}$). Based on all of the above, a three-step decision tree was constructed: (1) otolith Sr:Ca < 0.97 $\text{mmol}\cdot\text{mol}^{-1}$ and Ba:Ca > 0.014 $\text{mmol}\cdot\text{mol}^{-1}$ indicate freshwater experience (i.e., chemically typical fresh water); (2) otolith Sr:Ca > 1.14 $\text{mmol}\cdot\text{mol}^{-1}$ and Ba:Ca > 0.005 $\text{mmol}\cdot\text{mol}^{-1}$ indi-

cate freshwater (i.e., chemically untypical fresh water) or estuarine experience; (3) otolith Sr:Ca > 0.97 $\text{mmol}\cdot\text{mol}^{-1}$ and Ba:Ca < 0.005 $\text{mmol}\cdot\text{mol}^{-1}$ indicate marine water experience.

No attempt was made to define brackish and saline water reference values, because ambient Sr:Ca ratios approach marine values at low to moderate salinities (i.e., at 8–20 PSU; Kraus and Secor 2004; Tabouret et al. 2010), which limits the ability to distinguish between saline and brackish water habitats. Furthermore, vertical salinity stratification in the inner parts of Norwegian fjords (e.g., Tjomsland and Kroglund 2010) limits the usefulness of undertaking this task.

Inter-habitat movements of eel after their initial settlement were defined as a (i) unidirectional movement between freshwater and marine habitats (i.e., ≥ 1 -year-old marine water recruits entering fresh water or ≥ 1 -year-old freshwater recruits returning to marine habitats), (ii) one bidirectional movement (i.e., roundtrip) between freshwater and marine habitats (i.e., starting from either freshwater or marine habitat), or (iii) multiple bidirectional movements (i.e., two or more roundtrips) between freshwater and marine habitats (i.e., starting from either freshwater or marine habitat). A roundtrip is not confined temporally and can take several years to be completed. Additional methodological considerations and limitations of the data are discussed in Supplementary Material (Text S1).

Fisher's exact test of independence was used to determine if the distributions of marine water residents and inter-habitat shifters differed between marine water sampling locations. Differences in mean age and growth rate between location, sampling habitat (freshwater, marine water, and estuary) and habitat use patterns were tested with analysis of variance after the response variable was log-transformed to meet the assumptions of the analysis. Post-hoc comparisons for growth rate differences between sampling habitats and habitat use patterns were performed using Tukey's Honestly Significant Difference test. Statistics and data visualizations were carried out using the software R (R Core Team 2020, v.4.0.3), STATISTICA (v.7.0), and CorelDRAW Graphics Suite (v.12.0).

3. Results

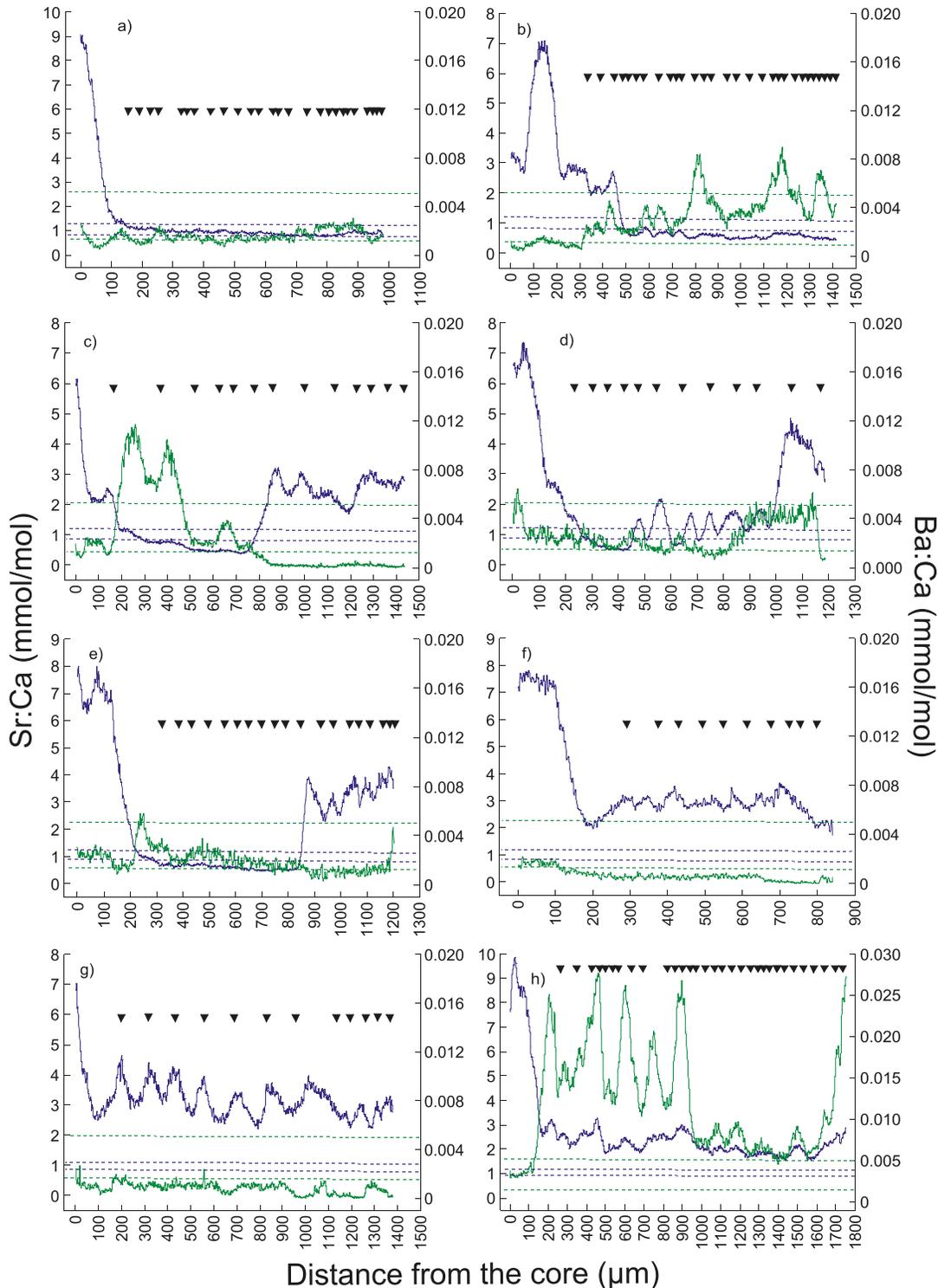
3.1. Water chemistry

Water chemistry analysis showed that freshwater lakes with unexpectedly high Sr:Ca and Ba:Ca ratios exist on the western coast of Norway (Table 2). In addition to Lake Fiskevatnet, similarly high Sr:Ca and Ba:Ca were observed in at least two other lakes on the Austevoll archipelago but not in the other sampled freshwater locations (Table 2).

3.2. Otolith microchemistry

Of the eel sampled in marine waters ($n = 371$), 80% were classified as marine water residents and 20% as inter-habitat shifters (Table 1; Figs. 3, 4). Of the inter-habitat shifters ($n = 76$), 47% initially settled in fresh water and 53% in marine water. Most inter-habitat shifters (57%) made multiple roundtrips (33% and 67% were freshwater and marine water recruits, respectively), although 15% made one roundtrip (all

Fig. 3. Representative examples of otolith Sr:Ca (blue line) and Ba:Ca (green line) profiles of European eel (*Anguilla anguilla*) sampled in marine and freshwater habitats in Norway: (a) 330 mm and 26-year-old freshwater resident eel from Botnelva; (b) 540 mm and 29-year-old freshwater resident eel from Litledalsvatn with a delayed freshwater entry at 3 years of age; (c) 650 mm and 16-year-old inter-habitat shifter eel from Grimstad with a delayed freshwater entry at one year of age; (d) 630 mm 12-year-old inter-habitat shifter eel from Bømlo with a delayed freshwater entry at one year of age; (e) 512 mm 19-year-old inter-habitat shifter eel from Smøla; (f) 440 mm 10-year-old marine water resident eel from Arendal; (g) 540 mm 12-year-old marine water resident eel from Etnefjord; and (h) 620 mm 30-year-old freshwater resident eel from Fiskevatn. Black triangles denote the otolith annuli positions on profiles. Otolith Sr:Ca (dashed blue lines) and Ba:Ca (dashed green lines) freshwater reference values are added to the plot. Lower blue dashed line—Sr:Ca upper limit for the chemically typical fresh water; lower green dashed line—Ba:Ca lower limit for the chemically typical fresh water; upper blue dashed line—Sr:Ca lower limit for the chemically untypical fresh water; and upper green dashed line—Ba:Ca lower limit for the chemically untypical fresh water.



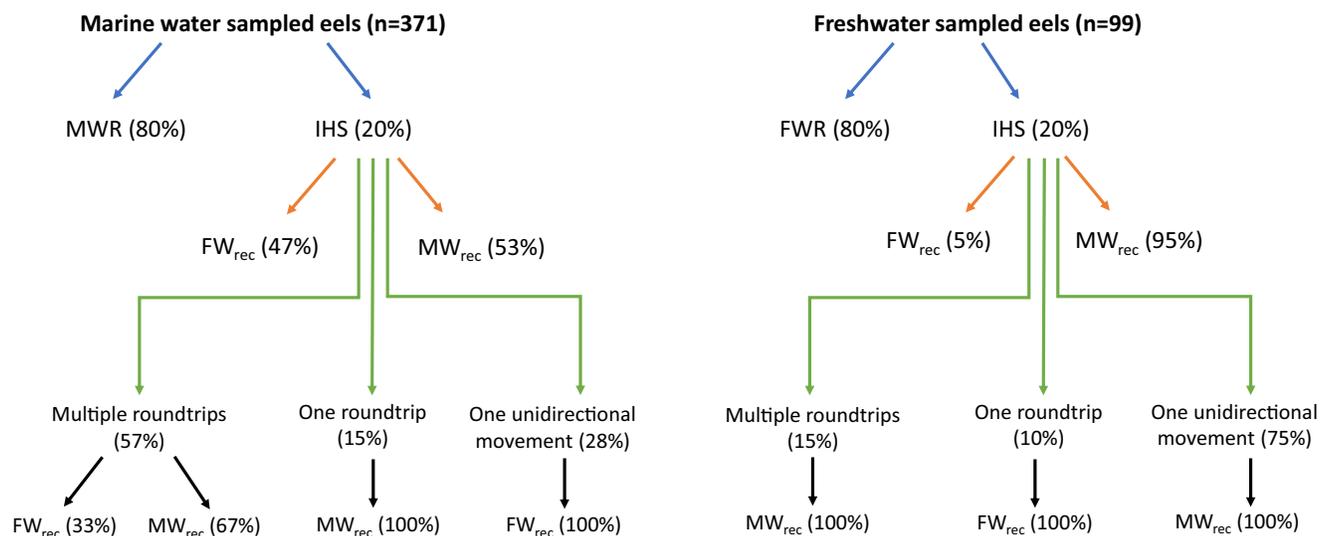
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Table 2. Concentrations of Ca, Sr, and Ba in water samples from freshwater locations in Western Norway.

Location	Coordinates	Ca	Sr	Ba	Sr:Ca	Ba:Ca
Fiskevatn	60.079°N 5.230°E	682	10.3	5.1	6.9	2.2
Tretlivatn	60.083°N 5.237°E	1200	14.1	9.6	5.4	2.3
Vassnesvatn	60.037°N 5.222°E	2999	22.2	6.3	3.4	0.6
Kolbeinsvik	60.067N° 5.207°E	916	12.8	5.1	6.4	1.6
Finnåsvatn	59.759N° 5.279°E	1533	6.8	1.0	2.0	0.2
Litledalsvatn	59.657N° 6.046°E	1274	6.7	4.0	2.4	0.9
Etne River	59.670N° 5.947°E	1257	5.6	3.4	2.0	0.8
Bårvågsvatn	59.634N° 5.495°E	816	7.0	3.4	3.9	1.2

Note: Concentrations of single elements are in $\mu\text{g}\cdot\text{L}^{-1}$ and ratios in $\text{mmol}\cdot\text{mol}^{-1}$.

Fig. 4. Graphical summary of the habitat use pattern variation among European eel (*Anguilla anguilla*) sampled in marine and freshwater habitats in Norway. MWR—marine water resident; IHS—inter-habitat shifter; FWR—freshwater resident; FW_{rec}—freshwater recruit (i.e., initial settlement as a glass eel in fresh water); MW_{rec}—marine water recruit (i.e., initial settlement as a glass eel in marine water).



were marine water recruits). Twenty eight percent of inter-habitat shifters made one unidirectional movement (all were freshwater recruits that returned to marine waters). Average age \pm SD at unidirectional movements was 12 ± 5 years (range = 3–23 years). Average age \pm SD at one-time roundtrips was 5 ± 5 years (range = 1–13 years) for freshwater entry and 9 ± 5 years (range = 2–19 years) for freshwater exit.

Proportions of marine water residents and inter-habitat shifters were significantly different between marine sites ($P < 0.0001$). No latitudinal gradient in the proportion of marine water residents was detected when all marine water sampling sites were included ($P = 0.7$; $R^2 = 0.03$). However, pro-

portion of marine water residents declined significantly towards the north when the Nidelva Estuary was removed from the analysis ($P = 0.048$; $R^2 = 0.51$).

Of the eel sampled in fresh water ($n = 99$), 80% were freshwater residents and 20% were inter-habitat shifters (Table 1; Figs. 3, 4). Of the inter-habitat shifters ($n = 20$), 95% initially settled in marine water and 5% in fresh water. Most inter-habitat shifters (75%) made one unidirectional movement (all were marine water recruits). Fifteen percent of inter-habitat shifters made multiple roundtrips (all were marine water recruits) and 10% made one roundtrip (both were freshwater recruits). Average age \pm SD at unidirectional movements was

3 ± 2 years (range = 1–8 years). Age at one-time roundtrips for the two individuals that had undertaken one roundtrip, and completed it within the same year, was 5 and 10 years.

3.3. Age and growth rate

Mean age of eel at sampling differed among locations ($F_{[12,454]} = 22$; $P < 0.001$) and between sampling habitats ($F_{[2,464]} = 58$; $P < 0.001$) (Fig. 5). Generally, estimated age of eel sampled in freshwater habitats (mean = 22 years) and the Nidelva Estuary (mean = 19 years) were higher compared to the estimated age of eel sampled in marine habitats (mean = 15 years). Mean age of eel sampled in marine habitats increased toward the north. Mean growth rate of eel differed among locations ($F_{[12,454]} = 100$; $P < 0.001$) and between sampling habitats ($F_{[2,464]} = 238$; $P < 0.001$; Fig. 6). Mean growth rate of eel from marine (mean = 34 mm·year⁻¹), estuarine (mean = 27 mm·year⁻¹), and freshwater (mean = 17 mm·year⁻¹) habitats all differed significantly from each other ($P < 0.001$; Tukey's HSD test). Growth rate of eel sampled in marine locations generally decreased with increasing latitude (except in Hardangerfjord, where one of the highest mean growth rates was observed, i.e., mean = 41 mm·year⁻¹). Mean growth rate of eel also differed between habitat use patterns ($F_{[3,463]} = 137$; $P < 0.001$). Generally, growth rate was significantly faster in marine water resident eel (mean = 35 mm·year⁻¹) compared to inter-habitat shifters (mean = 27 mm·year⁻¹) and freshwater resident eel (mean = 17 mm·year⁻¹) ($P < 0.001$; Tukey's HSD test).

4. Discussion

4.1. Otolith microchemistry

On average, 80% of eel sampled in marine habitats were marine water residents. This means that these individuals had initially settled in marine habitats as glass eel and never moved to fresh water later in life. Although 20% of eel sampled in marine habitats were inter-habitat shifters, only 9% of them had settled in fresh water as glass eel. This indicates that the marine water yellow eel population in Norway is not dependent on eel that initially enter and go on to settle in fresh water.

No information exists on eel total abundance difference between fresh- and marine water habitats in Norway or other countries. Regardless, commercial eel fishing in Norway has traditionally taken place mostly in marine waters (Thorstad et al. 2011). The extent of coastal habitats available for eel in Norway is vast (i.e., ~103 000 km of shoreline) compared to the number and surface area of freshwater habitats generally inhabited by eel, for example, out of 30 575 surveyed lakes, eel were registered in only 1773 (Foldvik et al. 2019). This, together with our results, indicates that marine water resident eel distributed along the Norwegian coast can make a substantial, but unaccounted for, contribution to the spawning stock of eel that return to the Sargasso Sea. That marine habitats could produce more eel spawners than freshwater habitats has been proposed before (Tsukamoto et al. 1998; Tsukamoto and Arai 2001).

The proportion of marine water resident eel at different marine sites varied from 23% to 100%, with less marine water residents in low-salinity and northern sampling sites. Previous studies on European eel habitat use have also reported large variation in the proportion of marine water resident eel. At the southern end of the distributional range, the proportions of marine water resident eel have varied between 44% in Gironde Estuary and 100% in different lagoons (Daverat and Tomás 2006; Capoccioni et al. 2013). At the mid and northern end of the distributional range, the proportions of marine water resident eel varies between 4% in Swedish west coast and 98% in marine loughs of Ireland (Limburg et al. 2003; Shiao et al. 2006; Lin et al. 2012; Sjöberg et al. 2017; Andersson et al. 2019; Arai et al. 2019). These results, combined with those presented here, stress the importance of using representative sampling in marine habitats (e.g., low-salinity areas and areas outside the direct impact zone of rivers have to be all considered). In addition to sampling habitat, eel developmental stage should be considered when designing a sampling plan. We sampled yellow eel of mostly >10 years of age and excluded silver eel—if the objective is to study location-specific patterns of habitat use then yellow eel are preferred because they are relatively stationary at older ages (Daverat and Tomás 2006; Daverat et al. 2011).

It has also been postulated that marine water resident eel should occur more frequently at higher latitudes where the productivity is higher in marine waters compared to fresh water (Tsukamoto and Arai 2001). We observed a latitudinal gradient in the relative proportion of marine water residents (i.e., less marine water residents, more inter-habitat shifters in the north), but only if the Nidelva Estuary site was removed from the analysis. The Nidelva Estuary was the only marine water site with significant freshwater input, and it was expected that the share of marine water residents would be lower there, because of greater freshwater influence that would increase the share of inter-habitat shifters. Therefore, when considering only marine water sites without significant freshwater input, our results are consistent with the suggestion advanced by Jessop et al. (2004) that the proportion of marine water resident eel would decline near the northern limit of the species' geographic range. We also conducted a survey of published and unpublished data on the proportions of marine water resident European eel (>28 marine water locations, including lower estuaries from 41°N to 63°N) but found no relationship with latitude (Supplementary Table S2¹).

Although we do not know which factors drive eel habitat use, it is likely that both ultimate (evolutionary) and proximate (physiological and environmental) factors are involved. As catadromy is an ancestral trait in temperate freshwater eels (Tsukamoto et al. 2002) and the glass eel gut is pre-acclimated to life in fresh water (Ciccotti et al. 1993), there is a genetic predisposition for the ability to colonize fresh water at an early stage (Gross et al. 1988; Edeline 2007; Aoyama 2009). However, there are also strong indications that the basal drive towards fresh water is conditional and that the initial settlement habitat may be determined by the condition of arriving glass eel (i.e., the low conditioned tend to stay in marine habitats) and the temperatures they encounter

Fig. 5. Age of yellow-stage European eel (*Anguilla anguilla*) sampled in marine (blue boxplots), estuarine (pink boxplot) and freshwater (green boxplots) habitats in Norway ordered by the increasing latitude of the sampling location. Horizontal black lines denote the median and red circles the mean. Upper and lower limits of the box denote 75th and 25th percentiles, respectively. Whiskers denote minimum and maximum values, and data points beyond these are outliers.

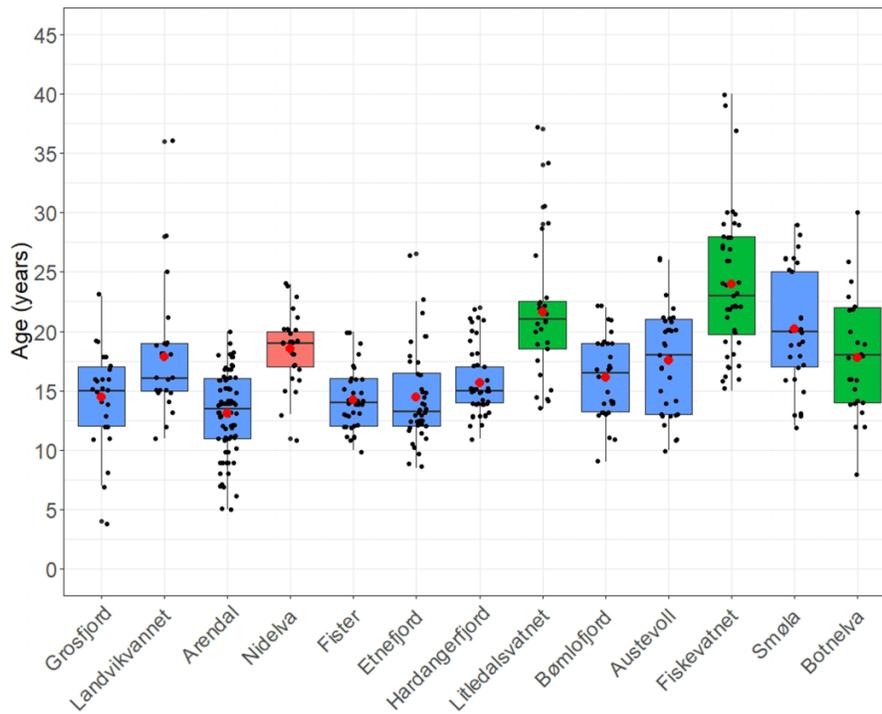
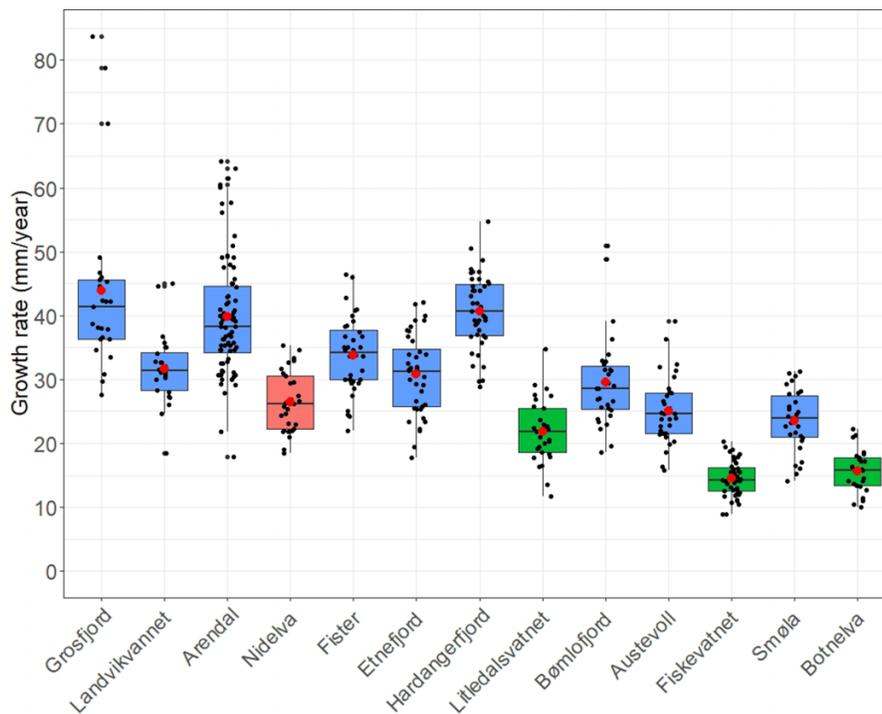


Fig. 6. Growth rate of yellow-stage European eel (*Anguilla anguilla*) sampled in marine (blue boxplots), estuarine (pink boxplot) and freshwater (green boxplots) habitats in Norway ordered by the increasing latitude of the sampling location. Horizontal black lines denote the median and red circles the mean. Upper and lower limits of the box denote 75th and 25th percentiles, respectively. Whiskers denote minimum and maximum values, and data points beyond these are outliers.



at critical transition points during their migration (Edeline et al. 2004, 2006; Imbert et al. 2008; McCleave and Edeline 2009; Sullivan et al. 2009; Liu et al. 2019). No relationship has as yet been reported between body condition and salinity choice in American or Japanese eels (Boivin et al. 2015; Fukuda et al. 2019). Eel leptocephali metamorphose into glass eel at the margins of the continental shelf (Tesch 2003), which may be ~1700 km away from the Norwegian coast. In addition to passive drift with the currents, glass eel then start to actively swim and orient themselves (Cresci et al. 2021), but they also stop feeding. We suggest that due to longer post-metamorphic migration to northern continental habitats and the concomitant greater energy expenditure, proportionally more glass eel will be in lower condition and will, therefore, be more likely to remain in marine habitats. Lower-latitude western European countries would receive more high-condition glass eel that will more likely recruit to and settle in fresh water. An initial preference for marine waters could also be promoted by the lower marine water temperatures at higher latitudes in spring compared to more southern areas, which would lower eel locomotor activity and restrict further movement inland to fresh water (Edeline et al. 2006).

Any habitat initially used by a juvenile eel might be re-evaluated later in life, as we show that on average 20% of eel undertook inter-habitat movements. We do not know why some eels move between marine and freshwater habitats. It is possible that eels shift habitats to gain access to better feeding sources and/or to escape severe winter conditions, as has been suggested for American eel (Clément et al. 2014). High levels of intra- and interspecific competition in marine habitats may force some eel to colonize freshwater habitats later in life (Moriarty 1978; Tsukamoto and Arai 2001; Edeline 2007). Although glass eel recruitment in the North Sea region has decreased by more than 95% (ICES 2020), we cannot exclude the possibility that they shift between habitats due to intraspecific competition, because data on eel abundance in Norwegian marine and freshwater habitats are lacking.

Inter-habitat shifting usually starts in marine water as on average 60% of inter-habitat shifters were marine water recruits. The proportion of marine water sampled inter-habitat shifting eels with initial freshwater or marine settlement was roughly equal. However, this was not the case for freshwater sampled inter-habitat shifting eels, in which 95% initially settled to marine water. This implies that a considerable number of eel had resided in marine habitats for variable periods (1–17 years) before their initial freshwater entry. In areas where glass eel immigration occurs, it is generally assumed that most if not all eel recruit to rivers as elvers (Feunteun et al. 2003; Tesch 2003; Daverat and Tomás 2006). In areas where only yellow eel immigration occurs (e.g., Eastern Baltic Sea), eel commonly enter fresh water at ages 1–10 years (Shiao et al. 2006). Delayed freshwater entry in areas with mainly glass eel immigration has also been observed in American eel. Specifically, 12%–25% of eel had recruited to the East River in Canada as yellow eel after 1–6 years in the estuary (Jessop et al. 2002, 2006). Therefore, it seems that delayed migration to fresh water is common in all north-

ern habitats that receive glass eels, but not in more southern latitudes.

4.2. Age and growth rate

The eel in Norway were generally younger and grew faster in marine habitats and at lower latitudes compared to freshwater habitats and higher latitudes, respectively. This is consistent with the general concept that eel grow faster in marine habitats than in freshwater habitats, although growth rate also increases with degree days (Daverat et al. 2012). Lower annual mean temperatures and shorter growth periods in northern compared to southern Europe translate into slower eel growth rates and eventually into a higher number of years needed to reach maturity. In general, eels mature at ages 10–25 and 5–15 years in northern and southern Europe, respectively. However, in northern Europe, female freshwater eel can mature at ages up to 39–57 years with mean age at maturity around 21 or 32 years, respectively (Poole and Reynolds 1996; Durif et al. 2020). Although we did not sample silver eel, yellow eel mean ages in marine sampling sites were approximately 13–15 years (maximum 36 years), but these increased to approximately 18–23 years (maximum 40 years) in freshwater sites. This, together with data from Durif et al. (2020), indicates that marine eel reach maturity sooner than freshwater eel in Norwegian waters.

Growth rate varied according to habitat use. Average growth rates of eel with a freshwater, marine water or habitat shifting profiles were 17, 34, and 27 mm·year⁻¹, respectively. Previous studies on eel growth rate in Norwegian marine and freshwater habitats have reported average estimates of 58 and 62 mm·year⁻¹, respectively (Vøllestad 1985; Vøllestad and Jonsson 1986). However, for fresh water, data from Vøllestad and Jonsson (1986) were recently re-evaluated and the new estimate was 30 mm·year⁻¹ (Durif et al. 2020), which is further corroborated by our data from other freshwater habitats in Norway. It is, therefore, likely that growth rate estimates from Vøllestad (1985) for marine water residents were also overestimated, because the same age reading methods were used in both Norwegian studies conducted in the 1980s. Other studies at northern latitudes have reported mean annual growth rates of 26–69 mm·year⁻¹ in freshwater (Lin et al. 2007; Simon 2007; Silm et al. 2017) and of 23–68 mm·year⁻¹ in marine sampled eels (Lin et al. 2007; Simon et al. 2013; Andersson et al. 2019; M. Rohtla, unpublished data). Mean eel growth rates at the southern areas of the distribution vary between 45 and 85 mm·year⁻¹ in marine and freshwater habitats (Daverat and Tomás 2006; Capoccioni et al. 2013). Therefore, eel growth rates are highly variable throughout the distributional range and dependent on local environmental conditions. Compared to eel in most of the eel distributional range, Norwegian eel grow relatively slowly and need more years to reach maturity. Although eel freshwater growth rates are generally lower (Daverat et al. 2012; present study) and parasitic threat is higher than in marine habitats, there are also benefits for freshwater resident eel such as somewhat greater energy stores and higher contents of certain essential fatty acids (e.g., arachidonic acid) that are key for maturation and reproduction (Parzanini et al. 2021a, 2021b). A thorough

analysis of growth was outside the scope of this study. It will be the subject of another study.

4.3. Conclusions and future perspectives

Marine water resident eel could represent a vital buffer system for the whole population, especially because catadromous eel endure additional pressures in fresh water (e.g., migration obstacles, habitat loss, and parasitic infestations). Therefore, accounting for marine eel can contribute to more informed stock assessments and management actions throughout their range. Our results draw attention to shallow coastal areas as important eel growth habitats that enable eel to grow, and most likely reach the silver stage, twice as fast compared to freshwater habitats. Considering that such shallow coastal areas are now also under high pressure with respect to anthropogenic modification and use, coastal management actions should take this new information into account. Our results on European eel in Norwegian waters also reinforce the general recommendation that rivers should be free of migration obstacles or that passages designed for eel should be installed to facilitate upstream migration of yellow eel and inter-habitat movements. Future studies should assess the absolute proportions of marine water resident, inter-habitat shifting, and freshwater resident eel at various latitudes throughout the distributional range. This can be achieved by sampling silver eel from open ocean sites near the coast (e.g., outer bay or fjord areas) or at geographical bottlenecks (e.g., Strait of Gibraltar, Strait of Dover, and Danish Straits) to obtain a more general estimate. Coupling this with estimates on glass eel condition, habitat productivity, and eel abundance would support an assessment of the ultimate and proximate factors that drive eel habitat use.

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Data available upon request.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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