Variability of habitat use by the European eel during its resident yellow eel life stage across the distribution range

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Abstract

The European eel (*Anguilla anguilla*) is a critically endangered species with a complex life history. The eel was previously described as an obligate catadromous fish (which hatch in marine water, spend the majority of their lives in freshwater, and then migrate back to spawn in marine water) but has in later years been reclassified as a facultative catadromous fish. The difference being that a facultative catadromous fish does not always migrate into freshwater. The habitat use of the yellow eel can be classed into freshwater residents, marine residents, brackish residents, and inter-habitat shifters. The aim of this study was to explore and assess the variability of the yellow eel's habitat use across its distribution range with a focus on habitat salinity. The study was conducted by gathering data from existing articles categorising habitat use based on Sr:Ca ratios in otoliths. After a screening of 99 articles, data analysis was conducted on results from 11 articles covering 10 countries. Of the 1290 sampled eels, 38% were freshwater residents, 26% were marine residents, 14% were brackish residents, 21% were inter-habitat shifters and, 1% were non-classifiable. Sample sizes and proportions of eels in each category varied greatly between countries.

Keywords: habitat use, otolith, inter-habitat shifters, resident eels, salinity

Sammanfattning

Den europeiska ålen (*Anguilla anguilla*) är en akut hotad art med en komplex livscykel. Ålen var tidigare klassad som en obligatorisk katadrom fisk (som kläcks i marint vatten, spenderar majoriteten av sitt liv i sötvatten och sedan migrerar tillbaka för att para sig i marint vatten) men har på senare tiden omklassificerats till en fakultativ katadrom fisk. Skillnaden är att en fakultativ katadrom fisk inte alltid migrerar till sötvatten. Habitatvalen hos gulålen kan klassas som levande i sötvatten, levande i marint vatten, levande i bräckt vatten eller habitat bytande. Syftet av denna studie är att undersöka och bedöma variationen av habitatval hos ålen genom hela sitt distributionsområde med fokus på val av salthalt. Studien gick ut på att samla data från redan existerande artiklar som kategoriserade habitat val baserat på Sr:Ca förhållanden i otoliter. Efter en screeningsprocess av 99 artiklar, utfördes dataanalys på resultaten från 11 artiklar som täckte 10 länder. Av de 1290 studerade ålar, levde 38% i sötvatten, 26% i marint vatten, 14% i bräckt vatten, 21% var habitat bytande och 1% var oklassificerbara. Provstorlekar och andel av ålar klassade i varje kategori varierade stort mellan länder.

Nyckelord: habitatval, otolit, habitatbyte, stationär ål, salthalt

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1. Introduction

1.1 Endangered status

The European eel (*Anguilla anguilla*), here after referred to as “eel”, is classified as a critically endangered species by the IUCN (the International Union for Conservation of Nature) Red List assessment (Pike & Gollock 2020). The abundance of eels has declined drastically over the last few decades despite ongoing conservation efforts (Pike & Gollock 2020). The main factors driving this decline are climate change, habitat fragmentation, pollution, overfishing and parasites (Drouineau et al. 2018). The number of glass eels arriving to Europe and north Africa greatly declined during the 1980s and has continued to remain low (ICES 2023). A better understanding of the European eel’s ecology may improve conservation efforts.

1.2 Life history

The Sargasso Sea, a western region of the Atlantic, was first suggested as a spawning site of eels by Johannes Schmidt during the 1920s (Schmidt 1923). However, it took an additional hundred years and the use of satellite tagging technology to track an adult silver eel’s migration to the presumed breeding grounds (Wright et al. 2022). The eel has a complex life cycle built up of multiple stages. The first stage, after hatching, is a transparent leaf shaped larvae, known as leptocephali (Schmidt 1923). The leptocephali are transported by currents in the Atlantic Ocean to Europe and north Africa (Schmidt 1923; Westerberg et al. 2018). As the leptocephali arrive at the coasts of Europe and north Africa they metamorphose into glass eels (Tesch & Greenwood 1977; Miller et al. 2015). Glass eels then develop pigment and metamorphose into elvers (Tesch & Greenwood 1977). At the next stage, the eel again shifts color, becoming a greenish yellow hue. This stage is called the yellow stage and is the growing phase (Schmidt 1923) which ranges from approximately 5 to 20 years or more (Miller et al. 2015). The European eel has a large distribution range, spanning from northern Africa and across most of Europe (Moriarty & Dekker 1997). Once the eel is ready to begin its journey for spawning in the Sargasso Sea, it will undergo its final metamorphosis and become a silver eel. The eel, now rich in fat, will stop eating (Schmidt 1923). The silver eel migrates back to its spawning site in the Sargasso Sea and the cycle begins anew (Wright et al. 2022).

The eel has traditionally been described as a catadromous fish. A catadromous fish spawns in marine waters whereafter it migrates into freshwater. The fish spends most of its life in freshwater rivers, lakes, and streams until it returns to marine waters to spawn (Daverat et al. 2006). However, in recent years, exceptions have been discovered, leading to the reclassification of the European eel from an obligate catadromous species to a facultative catadromous species (Daverat et al. 2006). The difference being that an obligate catadromous species always migrates as described above while a facultative catadromous species might never enter freshwater. Thus, facultative catadromy leads to a variation in behaviors within a species (Daverat et al. 2006). The eel can be divided into four main behavioral groups: marine resident, freshwater resident, brackish resident, and inter-habitat shifters. Resident eels stay in their habitat type for their entire yellow eel life stage, while inter-habitat shifters change habitat, often either once or on a regular basis (Feunteun et al. 2003; Daverat & Tomas 2006; Tabouret et al. 2010; Denis et al. 2023; Rohtla et al. 2023; Teichert et al. 2023). The majority of yellow eels have been found to be resident (Tzeng et al. 2000; Arai et al. 2006; Daverat & Tomas 2006; Lin et al. 2011; Teichert et al. 2022, 2023; Denis et al. 2023). This variation in habitat use is not due to locally adapted subpopulations, since whole-genome sequencing has shown that the eel is a panmictic population (Enbody et al. 2021).

1.3 Otolith microchemistry

Otolith microchemistry is a method that can be used to study past habitat use of migratory fish, including eels. The otolith, or ear stone, is a small, calcified part of the inner ear that is used for hearing and balance (Tabouret et al. 2010; NOAA Fisheries 2020). Otoliths grow throughout an organism's life during which trace elements from the surrounding habitat are integrated into the otolith (Durif et al. 2023). Freshwater has lower levels of strontium (Sr) than marine water. By analyzing the ratio of strontium to calcium (Ca) (Sr:Ca) in the otolith, one can determine which habitat types the fish has lived in (Tabouret et al. 2010). Habitat use can also be measured by other methods such as satellite or acoustic tagging but information on habitat use can only be gathered after the tagging has taken place. Habitat use prior to tagging cannot be derived from this method. However, otolith microchemistry allows for looking back in time at the life history of the fish from when they hatched until they were caught and the otolith was collected, allowing for retroactive assessment of habitat use. It is the only method currently available for studying the habitat use of the eel's entire life span. However, all eels that survive until they reach Europe or north Africa share the same life history in regard to habitat use (since they all hatch in the Sargasso Sea). Otolith microchemistry therefore only becomes informative after the elver stage (Durif et al. 2023). The yellow stage, being the longest and most variable in terms of habitat salinity (Schmidt 1923; Durif et al. 2023), gives the most interesting data about habitat use from otolith microchemistry. However, in order to study the otolith, it has to be removed from the fish, which is lethal. While this may be of little consequence for abundant fish species, it raises more concern when studying a critically endangered species such as the eel (Durif et al. 2023).

1.4 Research question

This study aims to explore the variability in habitat use by the yellow stage European eel (*Anguilla anguilla*) during its resident yellow eel life stage, throughout its distribution range. This study further aims to explore potential differences in habitat use between different regions. This will be done by gathering and comparing studies on habitat use. A data analysis will then be used to compare the distribution of eels in regard to habitat types and how that might differ in different countries. The purpose of the study is to gather and summarize key information about the yellow stage from various existing studies in order to further explain the eel's habitat use. The assumption is that increased knowledge of habitat use will aid the ecological understanding of the eel, which in turn may aid conservation.

2. Method

2.1 Data collection

Relevant articles were found by searching various databases accessed via the online libraries of Swedish University of Agricultural Sciences and Uppsala University, this gave access to over 300 databases, including PubMed, SCOPUS and Web of Science. Articles were also found with the search engine Google Scholar. Used search terms included: "otolith European eel", "otolith anguilla", "otolith habitat use", "habitat use European eel", "habitat use anguilla", "habitat use anguilla anguilla", "European eel yellow marine", "Life history of European eel" and "European eel yellow". Due to having a limited time frame, a systematic review was not conducted. Additional articles were found via the reference lists in articles that were found in the library databases and Google Scholar searches as well as through Google Scholar's feature to search for articles that have cited a specific article. Articles for which full text were not available through university access or Google Scholar were downloaded from Research Gate. Some articles were also provided by the supervisor Philip Jacobson.

A total of 99 articles were deemed potentially relevant based on their title. Titles were deemed relevant if they included the terms "European eel" or "Anguilla anguilla" or "Anguilla" or "Anguillid" as well as some indication that the article included information about habitat use, salinity preference or otolith microchemistry. After a full-text screening of these 99 articles, 11 were found to include information suitable for data analysis. These articles had to contain data from otolith microchemistry analysis of Sr:Ca ratios. Data from both yellow eels and silver eels were included since they both include data about yellow stage eels. Articles that tracked salinity of habitat by other methods, such as tracking devices on live eels, were excluded in order to increase comparability between studies. A brief summary of the articles method and results relating to habitat use were collected in a table.

Within the selected 11 studies there were differences in the wording used to describe habitat types. While some studies used the term inter-habitat shifters (sometimes written as interhabitat shifters or habitat inter-shifters) (Tabouret et al. 2010; Capoccioni et al. 2014; Denis et al. 2023; Rohtla et al. 2023) this was far from universal. "Nomads" was the most common alternative (Daverat & Tomas 2006; Capoccioni et al. 2014; Teichert et al. 2022). Several articles did not use a specific term but instead chose to only describe the process of habitat shifting (Tzeng et al. 2000; Arai et al. 2006; Lin et al. 2011). Two outlying terms were "mixed profile" (Teichert et al. 2023) and a study that distinguished between those who shifted habitat once in their lives and those who shifted more regularly (Limburg et al. 2003). The present study considered all abovementioned terms as describing the same general behavior and refers to them all as inter-habitat shifters. The term inter-habitat shifters was chosen over nomads due to it seeming like the more recent and popular term. Some articles (Arai et al. 2006; Tabouret et al. 2010) analyzing estuaries favored the categorization "estuarine" over brackish. The present study considers estuarine residents as brackish residents due to salinity, even if the term was not used in the original article. All but two studies used the term marine for one of their categories. One was a Swedish study that did not sample any marine resident eels and another was a Turkish study which instead used the term "sea water" (Lin et al. 2011). Sea water residents were, in this study, classified as marine residents. One study, Capoccioni *et al.*, (2014), included non-classifiable eels which were categorized as such. Another study looked specifically at restocked eels compared to natural recruits (Limburg et al. 2003), the restocked eels were excluded from data analysis due to their artificial life history.

2.2 Data analysis

All calculations were performed in Excel. Many of the articles used in this study presented their results in the form of percentages, rather than the exact number of eels in each habitat type. These percentages were used to calculate the number of eels in each habitat type (since the total number of sampled eels was known). However, this resulted in fractions of eels distributed in different habitats in some studies, likely due to these articles rounding off the presented percentage. I rounded off the calculated number of eels to whole numbers (integers). Due to some articles such as Teichert *et al.*, (2023) studying eels across large areas, data was grouped based on the country eels were sampled from rather than grouped based on study that the data was collected from.

The total number of eels in each habitat type was calculated by summing eels from all countries in the respective habitat categories. This total sum was converted into percentage by dividing by the total number of sampled eels. Due to the large variation of number of sampled eels which influenced this result, a second version was calculated that disregarded the variation of number of sampled eels. The "relative habitat use" (Table 1 and Fig. 4) was calculated by taking the average of the previously calculated percentage of eels in each habitat type in each country. A standard deviation (STANDEV.P) was calculated to visualize the variation of habitat use between countries.

2.3 Spatial coverage of relevant studies

Coordinates of sampling sites (locations where eels were collected) were found using Google maps (see coordinates in Appendix 1). Names of sampling sites, as well as any available maps in respective articles showing sampling sites, were used to corroborate that the correct location had been found. A map of the sampling sites was created using QGIS (version 3.34.3). Coordinates and sampling site names were imported as a delimited text layer. Data points were enlarged, and opacity was set to 30% in order to differentiate overlapping points.

3. Results

Results are based on data from 11 articles analyzing Sr:Ca levels in otoliths to determine the salinity levels that eels have inhabited (Tzeng et al. 2000; Limburg et al. 2003; Arai et al. 2006; Daverat & Tomas 2006; Tabouret et al. 2010; Lin et al. 2011; Capoccioni et al. 2014; Teichert et al. 2022, 2023; Denis et al. 2023; Rohtla et al. 2023). Data from otoliths from 1290 eels from 10 countries were analyzed. Most eels were collected from France and Norway (Fig. 1). The 66 sampling sites included in this study were distributed across most of the European eel's distribution area (Fig. 2). Coordinates for sampling sites are presented in Appendix 1.

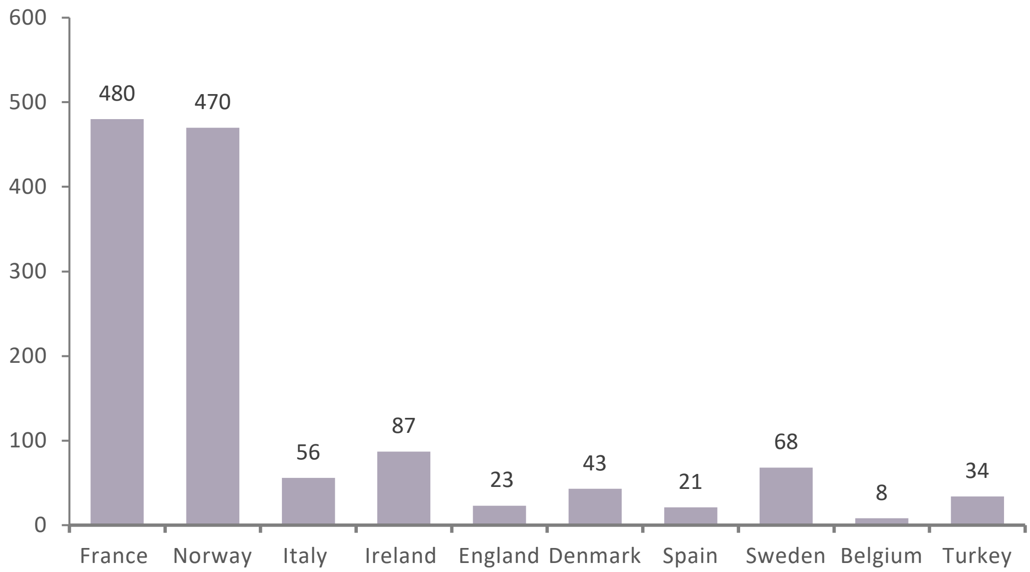


Figure 1 Number of eels collected in France, Norway, Italy, Ireland, England, Denmark, Spain, Sweden, Belgium, and Turkey

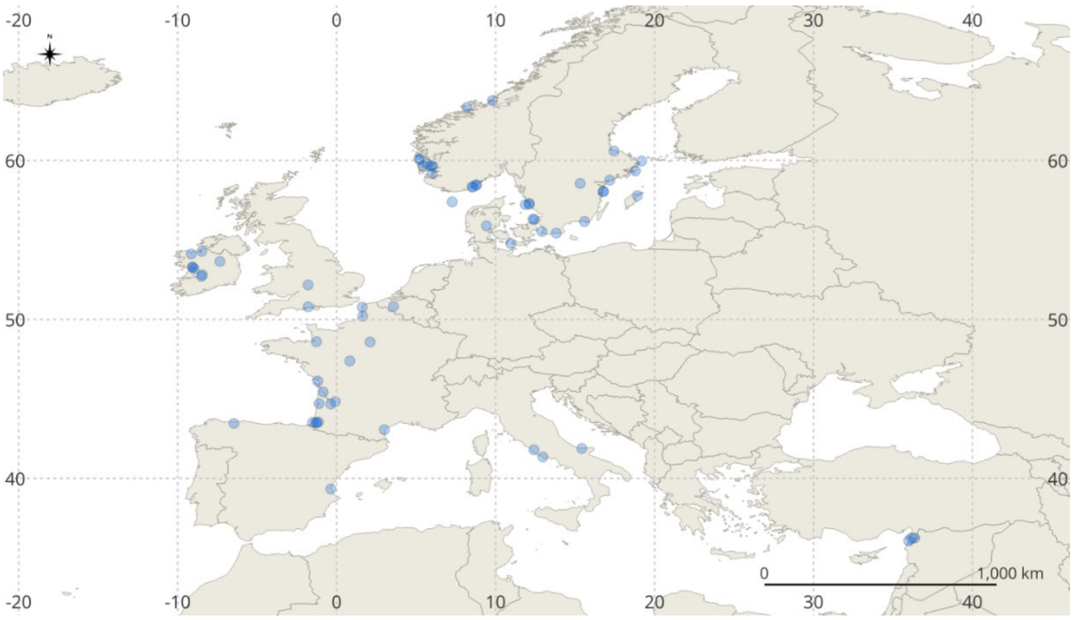


Figure 2. Map of the 66 sampling sites included in this study. One data point indicates one sampling site. Some data points appear darker due to multiple sampling sites in close proximity to each other, resulting in overlapping data points.

The cumulative results of all 11 studies, grouped by country, show that freshwater residents were the most common habitat category at 486 eels, a total of 38% of all sampled eels (Table 1). Marine residents were the second most common category at 333 eels, a total of 26%, followed by 271 inter-habitat shifters at 21%, 182 brackish residents at 14% and finally 18 non-classifiable eels at 1% (Table 1). All non-classifiable eels came from one sampling site, a lagoon in Italy (though not all eels from this sampling site were non-classifiable), the authors believe that the lagoon changes in salinity on a seasonal basis (Capoccioni et al. 2014). These eels were originally classed as inter-habitat shifters but upon further inspection believed by the authors of the study to be resident eels in water that shifts between brackish and marine (Capoccioni et al. 2014). Additional information on the number of eels found in each habitat type at each sampling site as well as the number of eels from each study is presented in appendix (Appendix 1).

Table 1. One row (apart from the three last rows) shows the habitat use (freshwater residents, marine residents, brackish residents, inter-habitat shifters and non-classifiable eels) in one country. Results are given in number of eels and percentage (percentage here refers to proportion of eels found in each country meaning that each country's total number of sampled eels is 100%). "Total" shows the total number of eels found in each habitat category as well as the total percentage of habitat use (where 1290 eels is 100%). "Average" is the average of each collum, meaning the average number of eels found in each habitat category and average percentage of eels in each habitat category. The final row shows the standard deviation of each collum (excluding the final three rows). The leftmost collum shows the studies from which the data was collected from.

Count-ry	**Fresh-water residents**		**Marine residents**		**Brackish residents**		**Inter-habitat shifters**		**Non-classifia-ble**		**Sour-ce**
France	49%	236	5%	26	26%	123	20%	95	0%	0	(Daverat & Tomas 2006; Tabouret et al. 2010; Teichert et al. 2022, 2023; Denis et al. 2023)
Norway	17%	80	63 %	295	0%	0	20%	95	0%	0	(Rohtla et al. 2023)
Italy	16%	9	0%	0	23%	13	29%	16	32 %	18	(Capoccioni et al. 2014)
Ireland	86%	75	10 %	9	0%	0	3%	3	0%	0	(Arai et al. 2006; Teiche

											rt et al. 2023)
England	83%	19	0%	0	0%	0	17%	4	0%	0	(Teichert et al. 2023)
Denmark	33%	14	5%	2	9%	4	13%	23	0%	0	(Limburg et al. 2003; Teichert et al. 2023)
Spain	29%	6	0%	0	52%	11	19%	4	0%	0	(Teichert et al. 2023)
Sweden	9%	6	3%	2	46%	31	43%	29	0%	0	(Tzeng et al. 2000; Limburg et al. 2003; Teichert et al. 2023)
Belgium	100%	8	0%	0	0%	0	0%	0	0%	0	(Teichert et al. 2023)
Turkey	94%	32	0%	0	0%	0	6%	2	0%	0	(Lin et al. 2011)
Total	**38%**	**486**	**26%**	**333**	**14%**	**182**	**21%**	**271**	**1%**	**18**	
Average (±1 S.D)	**52% (±34%)**	**49 (±68)**	**9% (±18%)**	**33 (±87)**	**16% (±19%)**	**18 (±36)**	**17% (±12%)**	**27 (±35)**	**3% (±10%)**	**2 (±5)**	

There was a variation in habitat use between countries (Table 1). Freshwater residents were the only category present in all countries, inter-habitat shifters where present in all countries except Belgium, marine residents and brackish residents were each present in half of the countries (Table 1 and Fig. 3).

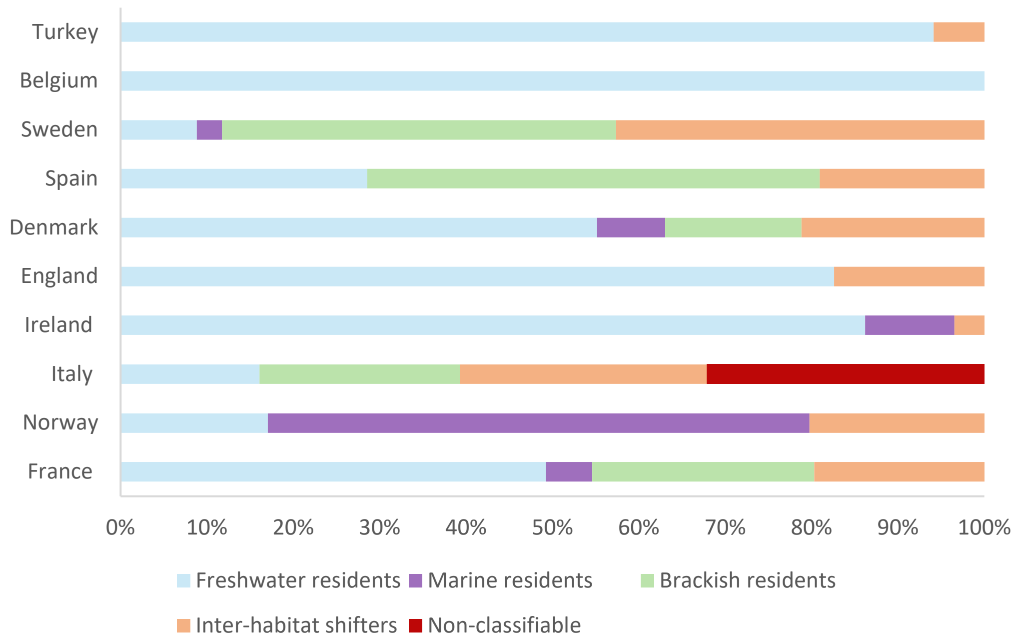
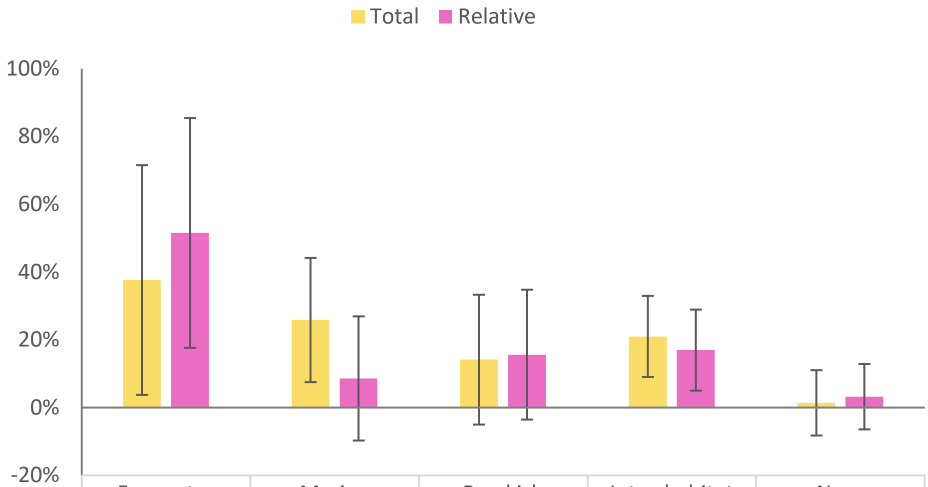


Figure 3. The percentage of habitat use for each of the 10 countries. Habitat use is divided into freshwater residents (blue), marine residents (purple), brackish residents (green), inter-habitat shifters (orange) and non-classifiable eels (red). Non-classifiable eels refer to those that could not be classed as any of the previously mentioned categories.

Due to the large variation in number of eels collected in each of the studied countries (Fig. 1), an additional calculation was made to determine the relative habitat use (Table 1). Relative habitat use refers to the calculated average percentage of eels in each habitat category. Relative habitat use describes the distribution of eels in each habitat type based on the proportion of eels in each habitat type in each country, instead of the total number of eels in each habitat type in each country. This means that it removes the variable sampling size. The main differences between the two are that relative habitat use has a larger proportion of freshwater residents and smaller proportion of marine residents as compared to total habitat use (Fig. 4).



	Freswater residents	Marine residents	Brackish residents	Inter-habitat shifters	Non-classifiable
Total	38%	26%	14%	21%	1%
Relative	52%	9%	16%	17%	3%

Figure 4. Percentage of eels in each habitat use category (freshwater residents, marine residents, brackish residents, inter-habitat shifters and non-classifiable eels) for both the total habitat use (yellow) and relative habitat use (pink). Total habitat use refers to the total percentage of eels in each habitat category. Relative habitat use refers to the average percentage of eels in each habitat category. Error bars show the standard deviation for each habitat category.

4. Discussion

In this study I found substantial variation in the habitat use of yellow stage eels regarding habitat salinity. Most eels were resident, whereof freshwater residents were the most common. A variation of habitat use was also found between countries. Freshwater residents were the only habitat type found in all countries. Inter-habitat shifters were found in all countries except Belgium (but only 8 eels were sampled there). Brackish and marine residents were each found in half of the sampled countries.

4.1 Variation between countries

The observed variation in habitat use between countries can be, at least in part, explained by the salinity of the sampling sites. Many of the French sampling sites were located inland while many Norwegian sampling sites were located on the coast (Appendix 1). This likely influenced the proportion of eels caught from each habitat type, suggesting that there is a sampling bias. If eels are sampled in freshwater there is a much higher chance of catching freshwater residents than there is of catching marine residents. However, due to the nature of otolith microchemistry and its ability to show past movements, not all eels caught in freshwater were classed as freshwater residents. Otolith microchemistry allows for the detection of inter-habitat shifters. While much less common, it is even possible to find an eel in freshwater whose otolith shows that it is a marine or brackish resident, if it had shifted to freshwater very recently (due to the shift not yet having been incorporated in its otolith) (Durif et al. 2023). The potential sampling bias could be investigated and mitigated by adding salinity of sampling site as a variable to see its effect on habitat use. Though, that would require more time than this project allowed for.

The sampling sites are most likely not random but rather areas of interest chosen by the authors and based on prevalence of eels. This would imply that the sampling sites give some indication of eel availability in given countries, though the small scale of sampling in some countries must be noted here. In a hypothetical scenario, where all waters in all countries were to be sampled equally, there would still likely be a variation of salinity of suitable habitats between countries. This means that the distribution of eels residing in freshwater, marine, and brackish waters likely vary between countries even without the sampling bias. This is presumably, at least in part, because of the variation in habitat availability. For example, France has many suitable estuaries and a significant proportion of their eel population reside in estuaries, while Ireland, which has fewer estuaries, thus has fewer estuarine eels (Arai et al. 2006; Denis et al. 2023). Instead, most eels in Ireland reside in either freshwater or marine water (Arai et al. 2006; Denis et al. 2023). This indicates that eels settle in waters based more on habitat availability than salinity. It is also worth noting that a variation was found within countries (see Appendix 1), which may also be explained by the differences between sampling sites within a given country.

4.2 Total distribution

The combined findings in this study show that the yellow eel displays variation in habitat use. However, when analyzing the results, it is important to note that most eels were sampled in France and Norway, rather than evenly throughout the distribution range. This leads to skewed results, were France and Norway have a disproportionate influence on the results. Results may therefore not accurately describe the behavior of yellow eels as a whole, but rather the behavior in these particular regions. This study also indicates that there is a lack of available otolith data regarding salinity choice in other regions, as fewer relevant studies were found that focused on southern Europe and no relevant studies were found that focused on north Africa. If France and Norway had been closer to each other their combined data may have given a more reliable result than one of them does on their own, however, they are relatively far from each other in relation to the eel's total distribution range. One can argue that considering the distribution of eels separately for each country would be more suitable. The downside of this is that the sample sizes are quite low in some countries. On the other hand, they are deemed reliable enough for the authors of those articles to present their findings as relevant and the results of all analyzed studies have been published in scientific journals. In an attempt to compensate for the variation of sample sizes an alternative calculation was made, disregarding the variation of sample sizes. The issue with this alternative calculation is that it places equal weight to smaller or partial studies such as Belgium. Only 8 eels were collected from Belgium as a part of a study conducted in multiple countries (Teichert et al. 2023). There is insufficient evidence to assume that a larger scale study in Belgium would follow the same habitat use distribution as was found in these 8 eels. Indeed, the authors do not claim that their data accurately represented Belgium's habitat use, only that that data is relevant when looked at in combination with their other data. Although this study also includes the other data collected in Teichert *et al.* (2023), it is not certain that it can be isolated from the rest in the manner done in this study. Another option would be to exclude the data from countries with smaller sampling sizes but that would have the drawback of reducing the total number of eels that the data is based on which would also reduce the reliability of the results. Throughout this entire study there is the issue of small sample sizes, which could be due to the high cost of otolith microchemistry and the lethality of extracting otoliths.

The occurrence of marine residents (26% or 9%), brackish residents (14% or 16%) and inter-habitat shifters (21% or 18%) are relatively similar. Even though freshwater residents (38% or 54%) were the most common category, it is not as dominant as it may appear at first if compared to the other habitat uses together. In the first calculation at 38%, the majority 62% of eels are not freshwater residents but instead made up of alternative life histories. This further supports the conclusion that eels are facultative catadromous fish rather than obligate catadromous fish. Even in the second calculation where freshwater residents make up 54%, this is only a little more than half of the eels following a classic catadromous lifestyle. Interestingly marine residents were the category that varied the most, both between these two calculations and between countries. This could be due to variations in access to suitable marine waters within the distribution range. When considering the results of this study, I find it surprising that the eel was reclassified as a facultative catadromous eel so recently (Daverat et al. 2006). Durif et al (2023) suggest that it is possible that declines in freshwater residents might be compensated for, at least in part, by an increase in the proportion of eels in other habitat categories. This implies that the proportion of freshwater residents are believed to be declining at a greater rate than others. It would therefore be interesting to study whether there has been a decrease in the proportion of freshwater residents over time. If the eel used to have a higher proportion of freshwater residents it could explain why it was originally classified as an obligate catadromous fish and why it was reclassified so recently.

In the present study, eel believed to be restocked (Limburg et al. 2003) were excluded from data analysis. There may however be eels in other studies that were, unbeknownst to the authors, restocked. This could increase the proportion of eels classified as inter-habitat shifters if the salinity of their original habitat did not correspond to the salinity they were relocated to. It also brings up a more critical question of whether the restocked eels from Limburg et al. (2003) should have been excluded in the first place. Restocked eels could be considered their own life history, despite their artificial nature. On the other hand, if restocked eels differ in behavior from other eels, it may affect the results. One can argue that natural eel behavior must be better understood before it can accurately be compared with restocked eels and thus understand how the two may differ. Given that restocking eels is a common practice (ICES 2023), excluding data from artificial life history could lead to results that describe the world less accurately.

In both Norway and France approximately 20% of studied eels were inter-habitat shifters. Similarly, the average percentage of inter-habitat shifters was 21% when looking at all data combined, though this result is heavily influenced by the large sample sizes of these two countries. The average percentage of inter-habitat shifters is 18% when comparing all countries equally. In combination, this could indicate that the percentage of inter-habitat shifters may be near 18-21%. However, there is a substantial variation between the amount of inter-habitat shifters found in different countries as can be seen by the high standard deviation. The standard deviation is high for all habitat categories indicating either that more data is needed to find the average proportion of respective categories or that the categories vary in proportion so much between countries that such a generalization should be avoided.

A smaller number of studies also presented more detailed information of inter-habitat shifters movements. Some eels shifted habitat only once in their life while others shifted habitat on a regular or seasonal basis (Tabouret et al. 2010; Ovidio et al. 2013; Williamson et al. 2023). There are also results of more inter-habitat shifters in one study moving upstream in an estuary rather than downstream (Denis et al. 2023). This study has too little information to draw any conclusions on inter-habitat shifters movements other than that there appears to be a variation in the number of habitat shifts.

4.3 Causes of variation in habitat use

The cause of variation in habitat use was not assessed in this study but there are several explanations of factors that potentially influence it. External factors such as habitat productivity is one suggested driver of inter-habitat shifting since residence in a more productive habitat can be correlated with faster growth rates. An eel in a less productive habitat may therefore shift to a more productive (and more favorable) habitat (Capoccioni et al. 2014). A more desirable habitat can also be associated with more competition. It is suggested that less competitive (often younger and smaller) individuals will choose less productive habitats due to less competition (Feunteun et al. 2003; Daverat et al. 2006). Estuaries (brackish) are generally considered more productive waters for eels (associated with faster growth and higher body conditions) (Edeline et al. 2005; Daverat et al. 2006; Capoccioni et al. 2014; Teichert et al. 2023). However, this is not always the case, as a study sampling eel in Mediterranean lagoons (in Italy) found no difference in growth rates of brackish residents, freshwater residents, or inter-habitat shifters (no marine residents were sampled) (Capoccioni et al. 2014). These conflicting results may be related to differences in habitat use on a geographic scale. It can also be linked to the lack of data from the eel's southern distribution area.

A latitudinal gradient has been observed where eels at higher latitudes tend to prefer brackish and marine water more than those at lower latitudes (Daverat et al. 2006). At lower latitudes, female eels also tend to grow faster and migrate as silver eels for spawning at younger ages than those in the north (Teichert et al. 2023). A study conducted in Algeria found that eels in north Africa seem to mature faster and have a shorter yellow eel life stage than those living in Europe (Tahri & Panfili 2023). The authors suggest environmental conditions as a cause to this geographical variation (Tahri & Panfili 2023). Similarly, eels in Turkey had a higher growth rate than those of more northern regions, which was suggested to be correlated to higher water temperatures (Lin et al. 2011).

The distribution of eels can also be linked to ecological theories such as Ideal Free Distribution (Acou et al. 2011) or Density Dependent Distribution (Feunteun et al. 2003). Overall, there is an indication that eel habitat use is more likely correlated to salinity rather than based on it. An eel may choose to shift to a habitat of a different salinity but the benefit of this has likely more to do with habitat productivity, which is associated with salinity, rather than caused by the salinity itself. The eel's ability to inhabit a variety of salinity levels can be linked to the species' ability to inhabit a vast and diverse distribution range (Capoccioni et al. 2014; Enbody et al. 2021). This may in turn be evolutionarily advantageous in allowing the European eel to quickly colonize new areas (Feunteun et al. 2003).

Anthropogenic barriers such as dams also block access to some freshwater habitats which reduces the likelihood of eels migrating into certain freshwaters (Tzeng et al. 2000; Tamario et al. 2019). This may be affecting the distribution of eels leading to eels that may prefer freshwater to reside in habitats of a different salinity. While there have been some efforts to ease the migration of eels past dams, many solutions such as eel ramps have been found to be ineffective (Tamario et al. 2019). The presence of dams and other barriers can lead to habitat fragmentation in practice similar to a loss of habitat due to its inaccessible status (even if the habitats themselves have not been damaged). The effect of dams on habitat use of yellow eel could be further studied by recording the distance to dams at sampling sites to determine if it is correlated to reduced freshwater residence.

Habitat use is sometimes referred to as habitat choice (Daverat et al. 2006; Durif et al. 2023), although, it can be questioned whether habitat use always is an active choice. In cases such as habitat fragmentation there may not be the option to enter certain habitat types. If a dam is blocking access to freshwater, it may not be suitable to conclude that that eel has chosen not to enter freshwater. Yet, there are still individuals that manage to pass dams and enter freshwater (Tamario et al. 2019), showing that it is not impossible. Passing a dam, or attempting to, could therefore be seen as a choice, and if it is, then not attempting to pass the dam would also have to be a choice. One could argue that the choice between survival and likely death is not a choice at all, but this would not explain why some eels are found attempting to pass dams. Even without anthropogenic pressures such as dams or altered habitats, the individual eel's ability to make decisions can be discussed such as a less competitive eels' ability to choose habitat. While the eel can physically enter highly competitive habitats this could increase the risk of predation (Feunteun et al. 2003). Daverat et al. (2006) uses the phrase "ability to change habitat" rather than habitat choice in certain contexts. Such a wording may more accurately describe the individual eel's situation when its options are limited.

4.4 Limitations of study

The data used for this project is limited by what I could find by searching accessible databases with a limited time frame of 10 weeks. It is highly unlikely that all relevant articles were found or included. Several of the found articles sampled a relatively low number of eels and/or stated that their study did not necessarily include all habitat uses in their sampled area (Tabouret et al. 2010). Many relevant articles that were found did not include desired information about otolith microchemistry such as information of the movements of inter-habitat shifters, which further limits this project. In some cases, the data was not recorded and in others the data was outside the scope of that study and therefore not fully presented.

4.5 Ethics

The use of lethal methods such as the collection of otoliths from critically endangered species can be critiqued. However, compiling and comparing already existing data based on lethal methods, such as has been done in this study, causes no harm to animals.

5. Conclusion

During its yellow eel life stage, the European eel displays a wide range of habitat uses. Most eels are resident though a notable proportion of eels are inter-habitat shifters. The majority of resident eels resided in freshwater regardless of whether the results were standardized to ignore the variation in number of sampled eels in each country or not. However, brackish, and marine resident eels also occurred at a relatively high proportion, supporting the classification of the eel as a facultative catadromous species. Inter-habitat shifters also appear to vary in habitat use but more data is needed to describe their movement patterns.

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Appendix 1

Table 1. The number of eels from each sampling site is classed as freshwater residents, marine residents, brackish residents, inter-habitat shifters and non-classifiable. As well as the number of eels from each sampling site and the source from which all data was collected. Note that results from some sampling sites have been combined. This was due to unclear information about which eels were sampled from which sampling site.

Country	Sampling site	Fresh-water Resid-ents	Marine resid-ents	Brack-ish resid-ents	Inter-habitat shifters	Non-clas-sifi-able	Nr of eel	Sou-rce
France	Wimereux	1	0	15	4	0	20	(Denis et al. 2023)
France	Somme	0	0	15	2	0	17	(Denis et al. 2023)
France	St Laurent de Gosse, Termi and Cauneille in Gave de Pau River	9	0	0	1	0	10	(Teichert et al. 2023)
France	Bages Sigean Lagoon	0	0	4	1	0	5	(Teichert et al. 2023)
France	Frémur River	2	0	0	1	0	3	(Teichert et al. 2023)
France	The Sélune River	72	0	2	0	0	74	(Teichert et al. 2022)

France	Redon, Adour Estuary	0	0	7	7	0	14	(Tabouret et al. 2010)
France	St Laurent de Gosse, Termi and Cauneille in Gave de Pau River	67	0	0	0	0	67	(Tabouret et al. 2010)
France	The Arcachon Bay, The Pertuis, The Gironde estuary, The Garonne and Dorodgne rivers	83	26	80	79	0	270	(Daverat & Tomas 2006)
Norway	Arendal	0	78	0	2	0	80	(Rohtla et al. 2023)
Norway	Nidelva Estuary	0	7	0	23	0	30	(Rohtla et al. 2023)
Norway	Grosfjord	0	21	0	4	0	25	(Rohtla et al. 2023)
Norway	Landvikvann-et	0	24	0	0	0	24	(Rohtla et al. 2023)
Norway	Fisterfjord	0	23	0	13	0	36	(Rohtla et al. 2023)
Norway	Litledalsvatn	21	0	0	9	0	30	(Rohtla et al. 2023)

Norway	Etnefjord	0	39	0	1	0	40	(Rohtla et al. 2023)
Norway	Hardangerfjord	0	33	0	9	0	42	(Rohtla et al. 2023)
Norway	Bømlofjord	0	27	0	4	0	31	(Rohtla et al. 2023)
Norway	Fiskevatn	43	0	0	1	0	44	(Rohtla et al. 2023)
Norway	Austevoll	0	26	0	7	0	33	(Rohtla et al. 2023)
Norway	Smøla	0	17	0	13	0	30	(Rohtla et al. 2023)
Norway	Botnelva	16	0	0	9	0	25	(Rohtla et al. 2023)
Italy	Tiber River	9	0	0	6	0	15	(Capoccioni et al. 2014)
Italy	Lagoon of Lesina	0	0	13	7	0	20	(Capoccioni et al. 2014)
Italy	Caprolace Lagoon	0	0	0	3	18	21	(Capoccioni

								et al. 2014)
Ireland	River Garavogue, Sligo. River Moy, Mayo. River Corrib, Galway. Galway Bay. River Shannon, Killaloe. River Shannon, Castleconn ell. Lough Derrevarag h	64	9	0	2	0	75	(Arai et al. 2006)
Ireland	Corrib River	11	0	0	1	0	12	(Teic hert et al. 2023)
Englan d	Hampshire Avon	12	0	0	0	0	12	(Teic hert et al. 2023)
Englan d	Warwickshir e Avon	7	0	0	4	0	11	(Teic hert et al. 2023)
Denma -rk	Gudenå	7	0	0	1	0	8	(Teic hert et al. 2023)
Denma -rk	Danish baltic	7	2	4	22	0	35	(Lim burg et al. 2003)
Spain	Rio Esva	6	0	0	4	0	10	(Teic hert et al.

								2023)
Spain	La Albufera de Valencia	0	0	11	0	0	11	(Teichert et al. 2023)
Sweden	Stockholm Archipelago	1	0	4	4	0	9	(Teichert et al. 2023)
Sweden	Bua	0	0	3	0	0	3	(Tzeng et al. 2000)
Sweden	Klagshamn	0	0	3	0	0	3	(Tzeng et al. 2000)
Sweden	Ystad	0	0	2	0	0	2	(Tzeng et al. 2000)
Sweden	Karlskrona	0	0	2	0	0	2	(Tzeng et al. 2000)
Sweden	Kvädöfjärden	0	0	2	0	0	2	(Tzeng et al. 2000)
Sweden	Motala ström	0	0	0	3	0	3	(Tzeng et al. 2000)
Sweden	Ången	0	0	1	0	0	1	(Tzeng et al.

								2000)
Sweden	Dalälven	0	0	1	1	0	2	(Tzeng et al. 2000)
Sweden	Vendelsöfjorden	0	0	2	0	0	2	(Tzeng et al. 2000)
Sweden	Kullen	0	0	2	0	0	2	(Tzeng et al. 2000)
Sweden	Kvädöfjärden	0	0	1	1	0	2	(Tzeng et al. 2000)
Sweden	Väddö	0	0	2	0	0	2	(Tzeng et al. 2000)
Sweden	Lake Fardume	2	0	0	0	0	2	(Tzeng et al. 2000)
Sweden	Exiting the Baltic	3	2	6	20	0	31	(Limburg et al. 2003)
Belgium	Scheldt River	8	0	0	0	0	8	(Teichert et al. 2023)
Turkey	Demirköprü	9	0	0	1	0	10	(Lin et al. 2011)

Turkey	Güzelburç	5	0	0	1	0	6	(Lin et al. 2011)
Turkey	Samandağ	18	0	0	0	0	18	(Lin et al. 2011)

Tabel 2. Coordinates for all 66 sampling sites. Note that the number of sampling sites is different than in table 1 due to table 1 combining data from some sampling sites. Table 2 instead shows all sampling sites separately with their respective coordinates.

Sampling site	Latitude	Longitude
Wimereux	50.7701	1.612563
Somm	50.2002	1.642148
Loire River	47.38328	0.835306
Bages Sigean Lagoon	43.061	2.993906
Frémur River	48.57772	2.103639
The Sélune River	48.60133	-1.26757
Redon	43.52675	-1.49895
St Laurent de Gosse	43.50496	-1.29973
Termi	43.50057	-1.24909
Cauneille in Gave de Pau River	43.54427	-1.14135
The Arcachon Bay	44.70221	-1.10429
The Pertuis	46.11854	-1.18703
The Gironde Estuary	45.441	-0.84634
The Garonne River	44.67388	-0.36828
Dordogne River	44.83521	-0.07609
Arendal	58.46064	8.777166
Nidelva Estuary	58.46579	8.797672
Grosfjord	58.33968	8.59831
Landvikvannet	58.32716	8.5087
Fisterfjord	59.16522	6.014017
Litledalsvatn	59.65882	6.046205
Etnefjord	59.66828	5.922871
Hardangerfjord	59.78669	5.724271
Bømlofjord	59.65195	5.412797
Fiskevatn	60.06792	5.237509
Austevoll	60.10048	5.178654
Smøla	63.33784	8.193954
Botnelva	63.7661	9.799791
Tiber River	41.80021	12.41511
Lagoon of Lesina	41.88202	15.42324
Caprolace Lagoon	41.34914	12.97501

River Garavogue	54.27755	-8.47944
River Moy	54.11816	-9.14572
River Corrib, Galway	53.29607	-9.07453
Galway Bay	53.18281	-8.96819
River Shannon, Killaloe	52.80941	-8.44573
River Shannon, Castleconnell	52.71384	-8.50571
Lough Derrevaragh	53.64264	-7.34028
Corrib River	53.27557	-9.05603
Hampshire Avon	50.79078	-1.79522
Warwickshire Avon	52.16679	-1.79103
Gudenå	55.88674	9.430323
Rio Esva	43.45685	-6.46149
La Albufera de Valencia	39.33199	-0.36639
Stockholm Archipelago	59.34091	18.79846
Bua	57.24039	12.11413
Klagshamn	55.5329	12.91082
Ystad	55.42626	13.82273
Karlskrona	56.15708	15.5958
Kvädöfjärden	58.0482	16.77923
Motala ström	58.55407	15.32138
Ången	58.75689	17.1805
Dalälven	60.60094	17.44869
Vendelsöfjorden	57.30076	12.1163
Kullen	56.30723	12.35205
Kvädöfjärden	58.0482	16.77923
Väddö	59.95745	19.18423
Lake Fardume	57.7845	18.91755
Scheldt River	50.8213	3.576052
Demirköprü	36.24869	36.35505
Güzelburç	36.24669	36.1972
Samandağ	36.06813	35.99065
Kullen	56.2861	12.43107
Fladen	57.22514	11.86638
Skagerrak	57.39175	7.269307
Near islands Lolland and Falster	54.77968	10.96008

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