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The evolving story of catadromy in the European eel (*Anguilla anguilla*)

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Anguillid eels were once considered to be the classic example of catadromy. However, alternative life cycles have been reported, including skipping the freshwater phase and habitat shifting between fresh, brackish, and saltwater throughout the growth phase. There is a lack of knowledge regarding these alternate life strategies, for example, the proportion of individuals in the population that adopt them compared to classic catadromy. We provide a description of these alternate life cycle strategies in temperate anguillids, their possible drivers, and the methods available to investigate them. These methods (lethal and non-lethal), include otolith microchemistry, fatty acid and stable isotope analyses, parasite identification, blood transcriptomics, and electronic tags. We argue that since the current management framework for the European eel and other temperate eels is based mainly on the freshwater component of the population, it ignores eels growing in saline waters. Many of the factors that are thought to be responsible for the precipitous decline of the eel population are more prevalent in freshwater systems. Therefore, the contribution of saline eels may be more important than currently estimated. The habitat-shifting ability of eels may be all the more crucial for the persistence and recovery of those species that are endangered.

Keywords: blood transcriptomes; conservation; diadromy; fatty acid; marine residency; otolith microchemistry; parasite; phenotypic plasticity; stable isotopes

Introduction

Catadromous fish complete most of their feeding and somatic growth in freshwater ecosystems but spawn in marine waters. The habitat shifts that occur during the life cycle require energetically costly biochemical, physiological, and behavioural adaptations (Hutchinson, 1967). In catadromous species, there is large within-species variation in the timing of migration, life history strategies, and the prevalence of habitat switching. There is a long-standing debate among fish biologists over why individuals express different patterns in these traits, and to what degree the variation is genotypic or plastic in origin (Bloom and Lovejoy, 2014 and references therein). The study of phenotypic plasticity in life history and behaviour in fish has increased more than tenfold since the late 1990s. Variation among individuals does not simply describe “noise” around some theoretically predicted optimal life history strategy (Hutchings, 2021). Rather, it represents a valuable source of information for understanding behavioural plasticity and major evolutionary trade-offs in general and

also in catadromous fish (e.g. Hendry *et al.*, 2004; Haraldstad *et al.*, 2018).

Anguillid eels were once considered the classic example of catadromous fish. Eel species inhabiting temperate regions were thought to spend most of their life cycle growing in brackish or freshwater habitats before spawning in the open ocean, often thousands of kilometres away. The tolerance of eels to different temperature, depth, and salinity conditions is exceptional among fish. In addition to being found in rivers and lakes up to 1000s of km from the sea, they are present in all types of coastal habitats, including marshes, brackish water, lagoons, and fjord systems (Bertin, 1941; Tesch, 2003). Until the late 1990s, it was assumed by most researchers that all catadromous eels included a fresh- or brackish-water period in their life cycle. However, the advent of otolith microchemistry techniques demonstrated that some European and Japanese eels (*Anguilla anguilla* and *A. japonica*, respectively) collected in saline habitats (i.e. salt or

brackish waters) showed no evidence of a period of freshwater residency and displayed facultative catadromy (Tzeng *et al.*, 1997; Tsukamoto *et al.*, 1998). Yellow eels can, in fact, complete their growth phase and mature into silver eels without a freshwater phase (Tzeng *et al.*, 2000; Tsukamoto and Arai, 2001). Using the same otolith microchemistry techniques, more diverse behaviours were subsequently uncovered, including individuals known as habitat shifters, which undertake several migrations between fresh, brackish, and saltwater during their lifetimes (Tzeng and Tsai, 1994).

The European eel is found in Iceland, northern Norway, and northwest Russia, and all the way to the Mediterranean coasts and northwest Africa, in the south. All European eels spawn in the Sargasso Sea meaning that this species undertakes the longest migration of all anguillid eels—up to 8000 km (Vøllestad, 1992; Wright *et al.*, 2022). The species has been steadily declining for the past 50 years and is listed as critically endangered by the International Union for Conservation of Nature (IUCN) criteria (Dekker, 2004; Pike *et al.*, 2020). Hazards and threats that may be responsible for the decline apply to all life stages and include habitat loss and fragmentation, mortality from hydro-electric turbines, fishing activities, pollution, parasitic infections, and the negative effects of global warming on larval recruitment (Miller *et al.*, 2016; Drouineau *et al.*, 2018).

Management advice for *A. anguilla* is formulated, in Europe, within the International Council for the Exploration of the Sea (ICES), the European Inland Fisheries and Aquaculture Advisory Commission (EIFAAC), and the General Fisheries Commission for the Mediterranean (GFCM) delegations. The status of the population is evaluated based mainly on the recruitment of glass eels (juveniles) to freshwater and on the emigration of silver eels (spawners) to the sea. Thus, the current management framework is based on the freshwater component of the population (ICES, 2009). Alternate behaviours, such as eels remaining in saline waters or habitat shifting, are, importantly, not currently accounted for in the annual advice from ICES. Very few data on eel from saline waters are included in population assessments.

Although we know from the geographic distribution of fisheries that many eels grow and mature in saline waters, there is uncertainty regarding the relative proportion of freshwater vs. marine water residents. One of the reasons for this is linked to the difficulties associated with establishing sampling strategies for eel in the sea, especially to assess recruitment of year-classes arriving from the Sargasso Sea (ICES, 2009; Harrison *et al.*, 2014). The apparatus and associated techniques involved in catching eels during their upstream and downstream movements in a river are well established (e.g. traps, weirs, or nets) and easier to implement compared to sampling eels at sea where they are distributed across large and structurally complex habitats. Therefore, current assessments of eel in marine waters usually rely on commercial fisheries data to estimate the standing stock of yellow eels, or, in some cases, on labour-intensive scientific surveys (Durif *et al.*, 2011; Harrison *et al.*, 2014; Dorow *et al.*, 2021; Dorow *et al.*, 2023). When eels are caught in the sea, it is not known whether they have just arrived, are on their way to colonizing freshwater habitats, or have settled in the marine environment for their growth phase. This further complicates the assessment of the marine component of the population.

The aim of this paper is to highlight the importance of assessing marine residency and facultative catadromy in the

European eel. We provide an overview of the current knowledge on these topics, mainly concerning the European eel, but some examples will be taken from the closely related species such as Japanese and American (*Anguilla rostrata*) eels. We also aim to describe methodological approaches that are available to study alternate life cycle strategies linked to marine and coastal habitats. We discuss how improving our knowledge of the ecological role of eel living in marine habitats and the long-term dynamics of catadromy in anguillid eels constitutes a unique and important contribution to the management and conservation of these species.

The alternate life strategies of the European eel

The life cycle of the European eel is more complex than previously described (Tzeng *et al.*, 1997; Tsukamoto *et al.*, 1998; Robson *et al.*, 2012). Up to five different contingents (i.e. groups of eels sharing similar patterns of habitat shifts) have been described, based on the durations of residence in different habitats (Jessop *et al.*, 2002; Tzeng *et al.*, 2002; Daverat *et al.*, 2006). In most regions, eels colonize freshwater systems upon their arrival at the edge of the continent. “Freshwater residents” only leave the freshwater habitat once they become silver eels, migrating back to the spawning area. Some eels (up to 85–100% in some studies), hereafter referred to as “marine residents”, do not enter freshwater systems, remaining instead in marine or brackish water during their entire lives (Tsukamoto *et al.*, 1998; Limburg *et al.*, 2003; Lamson *et al.*, 2006). Other individuals, referred to as “habitat shifters”, move between marine and freshwater habitats several times during their growth phase (Daverat *et al.*, 2006; Marohn *et al.*, 2013; Benchetrit *et al.*, 2017; Rohtla *et al.*, 2023). When eels migrate into freshwater habitats, they mostly do so within the first two years after their trans-oceanic migration (Jessop *et al.*, 2002; Tzeng *et al.*, 2002). However, movements into freshwater can also occur later, at the yellow eel stage, sometimes even in eels up to 10 years old (Jessop *et al.*, 2006; Shiao *et al.*, 2006).

Adding even more complexity, some eels may perform short seasonal incursions into alternate habitats (Clément *et al.*, 2014). For instance, telemetry studies have revealed seasonal movements within the different parts of an estuary, where eels overwinter in the freshwater part (Thibault *et al.*, 2007). Similarly, otolith analyses have demonstrated short overwintering periods by eels in freshwater habitats (Clément *et al.*, 2014).

The drivers of marine residency

The high productivity of marine environments at temperate latitudes compared to freshwater environments could ultimately explain the evolution of anadromy (Gross *et al.*, 1988), and may also be an incentive for marine habitat use by eels. Anguillid eels are considered to have originated in the tropics (Tsukamoto *et al.*, 2002; Inoue *et al.*, 2010). Catadromy presumably evolved because of the higher productivity, which, in the tropics, is typically found in freshwater habitats rather than marine habitats (Gross *et al.*, 1988; Tsukamoto and Arai, 2001). The migratory plasticity of eels would result from a trade-off between aiming for the use of the most productive habitat and avoiding competition, and predation, which for eels are higher in brackish and marine waters (Edeline, 2007).

Research efforts to understand the proximate drivers for glass eels to settle in either saline or freshwater habitats have mainly focused on the effect of temperature and the relationship with body condition when glass eels arrive; however, additional drivers likely play key roles.

Glass eel migration consists of two phases (Harrison *et al.*, 2014). During the first phase, as they approach the continent and migrate through estuaries, glass eels use selective tidal stream transport (STST) (McCleave and Kleckner, 1982; Gascuel, 1986). Their ability to migrate against the flow is limited (Wuenschel and Able, 2008), and they instead save energy by remaining near the bottom during ebb tides and moving into the water column during flood tides (Harrison *et al.*, 2014 and references therein). In areas with little or no tide, glass eels require considerably more energy to advance (Beaulaton and Castelnaud, 2005). High body condition is important to support a continued upstream migration particularly at high river flows.

The second migration phase corresponds to active counter-current movement at the freshwater interface or downstream of obstacles where glass eels/elvers accumulate (Creutzberg, 1961; Tesch, 2003; Harrison *et al.*, 2014). Water temperature is the most important factor stimulating this active migration, which is exemplified by the typical creeping of glass eels and elvers over obstacles (Legault, 1988; McGovern and McCarthy, 1992). The swimming capacity of glass eels depends on water temperature (Tosi *et al.*, 1990; Edeline *et al.*, 2006). Active upstream movements rarely occur at temperatures <10°C (Hvidsten, 1985; Gascuel *et al.*, 1995; White and Knights, 1997; Beaulaton and Castelnaud, 2005; Laffaille *et al.*, 2007; Hwang *et al.*, 2014). On the south-western coast of Norway, glass eels arrive in the spring between March and April. At this time of year, temperatures in freshwater are still relatively cold, and glass eels typically wait in saline habitats until the water temperature exceeds 8°C (Skiftesvik, 1984; Cresci *et al.*, 2017). While glass eels have a threshold for swimming of ~4–7°C, they require higher temperatures, 12–14°C, for climbing vertical obstacles such as waterfalls (Linton *et al.*, 2007). If these temperature thresholds are not reached, and depending on the local topography, glass eels may not be physically able to migrate upstream into freshwater in some years. It is likely that body condition (i.e. energy storage) explains intraspecific variability in temperature thresholds for upstream migration.

Migrating into freshwater systems is energetically costly due to the physical effort but also due to the physiological changes required to modify the osmoregulatory system. Laboratory experiments have confirmed the tendency for glass eels with lower body condition to prefer saltwater over freshwater (Edeline *et al.*, 2006). In another laboratory study of the closely related species *A. japonica*, glass eels were more attracted to freshwater when water temperature was higher (20 vs. 13°C) (Fukuda *et al.*, 2019; Kumai and Kuroki, 2021). Therefore, it appears that two important factors favouring upstream migration and attraction to freshwater are high water temperature and body condition. Although this has not been demonstrated in the wild, the laboratory studies described above lead us to predict that glass eels with lower body condition would preferentially settle in the marine habitat. This would imply that eels with the longest migration route, and probably lowest body condition, would be marine residents (Rohtla *et al.*, 2023).

Geographical distribution of marine residency

Since productivity differences between freshwater and marine environments are not constant along latitudinal gradients, different incentives for the use of these habitats are likely to exist along the gradient. In general, higher latitudes have more anadromous species, and lower latitudes have more catadromous species (Gross *et al.*, 1988; McDowall, 1997). Latitudinal shifts in migratory behaviour are observed in other diadromous fish, for example, in salmonids (e.g. Hendry *et al.*, 2004). Brown trout (*Salmo trutta*) tends to be anadromous in cooler, boreal waters, while further south the species tends to abandon anadromy and becomes restricted to freshwater (McDowall, 1997). Similarly, Arctic charr (*Salvelinus alpinus*) displays great variability in anadromous behaviour. Anadromy is the minor density-dependent strategy for this species in southern Canada (Doucett *et al.*, 1999), but it becomes the dominant strategy throughout the middle part of the North American geographic range, and forgoing anadromy altogether at the northern limit of its distribution (Power *et al.*, 2008). Such latitudinal trends can be explained, at least in part, by phenotypic plasticity, as demonstrated by the observation that translocating salmonids to cooler locations induces anadromous behaviours (Thorpe, 1987; McDowall, 1997; Nordeng and Bratland, 2006). The reverse can also occur, for example, anadromous Chinook salmon *Oncorhynchus tshawytscha* stopped migrating when introduced into lakes in New Zealand (McDowall, 1990).

There is some support for a latitudinal gradient in the prevalence of catadromous profiles in eels (Daverat *et al.*, 2006; Jessop *et al.*, 2008; Rohtla *et al.*, 2023). For instance, the duration of the growth season for eels varies with latitude (Jessop, 2010; Daverat *et al.*, 2012), and this variation will be accentuated in freshwater compared to the sea where temperature conditions are more buffered. In northern Europe, temperatures decrease earlier in freshwater than in the sea, resulting in a relatively shorter growing season in freshwater than at sea at the same latitude. This is consistent with the observation that marine residency is especially important at the northern limit of the geographic distribution, where it may offer better growth opportunities than in oligotrophic freshwater systems (Cairns *et al.*, 2004; Lamson *et al.*, 2006; Jessop *et al.*, 2008). The long-standing tradition for small-scale shallow-water trap fisheries for yellow eels in the coastal waters of southern Norway, Sweden, and Denmark also supports this possibility (Scott, 1918; Ojaveer *et al.*, 2007). However, marine residents are also common in the southern part of the distribution, at least for the European eel found in lagoons in south-western France and in the Mediterranean (Acou *et al.*, 2003; Daverat and Tomas, 2006; Martinez-Carrasco *et al.*, 2011; Panfili *et al.*, 2012; Filippi *et al.*, 2013; Capoccioni *et al.*, 2014; Aschonitis *et al.*, 2017; Glamuzina *et al.*, 2022). This may be explained by the role of water temperature on habitat preference. While low temperatures in rivers may prevent glass eels from migrating into freshwater in the north (see above), high temperatures in the south may cause thermal stress and hinder somatic growth (Domingos *et al.*, 2006). In extreme conditions, some rivers may dry out during the summer, leaving only estuarine habitats as available refugia (Podda *et al.*, 2020). The high productivity of coastal Mediterranean lagoons may prompt some eels to settle in saltwater rather than colonize poorer upstream habitats (Capoccioni *et al.*, 2014). Compared to freshwater habitats,

brackish and marine habitats have a greater capacity to buffer extreme climatic events and offer a more stable growing environment for eel at the extremes of its distributional range. In the context of global warming, this may rapidly favour marine residency.

Marine residency and facultative catadromy in eels have been understudied and are overlooked. Since the pioneer articles in 1997 and 1998 (Tzeng *et al.*, 1997; Tsukamoto *et al.*, 1998), only 48 articles have been published on the two topics. Due to the difficulty of measuring recruitment in the marine habitat, glass eel recruitment is only assessed in freshwater habitats, thereby ignoring the fluctuations and parallel (or not) dynamics of freshwater and marine eel contingents. Methods for assessing facultative catadromy are available, which we describe in the following sections.

Methods available to detect and characterize marine residency and facultative catadromy in eels

Analyses of otolith microchemistry

The study of trace elements in the biogenic carbonates of otoliths can provide detailed information about the temporal extent of saline habitat use by eels (Campana, 1999; Elsdon *et al.*, 2008). The method is based on the premise that the chemical composition of freshwater differs from marine water in a predictable way. The combination of strontium to calcium ratio (Sr: Ca) and barium to calcium ratio (Ba: Ca) shows the best performance to trace fish movements across salinity gradients with the former being larger in marine water than in freshwater, and the latter being smaller in marine water than in freshwater (Tabouret *et al.*, 2010; Daverat *et al.*, 2011; Rohtla *et al.*, 2023). Otolith Sr: Ca and Ba: Ca offer a good resolution for salinities up to 20 ppt (Tabouret *et al.*, 2010), but this is probably location specific. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio is well suited to discriminating freshwater sites and, therefore, can provide higher resolution in estuarine habitats (Hobbs *et al.*, 2010), although it has rarely been used to infer movements of eels. The chemical differences in the water are incorporated into the otolith in proportion to their ambient availability as the fish moves through different salinity habitats (Elsdon *et al.*, 2008; Walther *et al.*, 2017; Hussy *et al.*, 2021).

Various qualitative and quantitative statistical methods have been developed to characterize eel migratory behaviours from otolith chemical profiles (e.g. Tsukamoto and Arai, 2001; Daverat and Tomas, 2006; Fablet *et al.*, 2007). Qualitative methods are based on threshold values of tracers and expert evaluation, while quantitative methods treat microchemistry data as time series. To date, otolith microchemistry remains the only tool available to uncover the salinity history of eels over their entire lifespan. However, this method also has some disadvantages, such as the need to sacrifice animals. It is also time-consuming, involving several steps to prepare and analyse otoliths. Short seasonal migrations occurring during the winter are not recorded in the otolith when temperatures are low and somatic growth is minimal (Thibault *et al.*, 2007; Clément *et al.*, 2014). Further, the edge of the otolith—the last year of the eel's life—is sometimes difficult to analyse because of the shape of the otolith. As eels grow older, their otoliths tend to become more concave (the edges grow more inwards). The growth increment on the otolith

also decreases with age and the annuli become more difficult to isolate. Hence, the most recent habitat changes may be overlooked. Preparing the otolith using a transversal section should avoid this bias and is therefore recommended for older individuals.

Discrepancies between the microchemistry signature at the edge of the otolith and the location of capture have been observed (Jessop *et al.*, 2012). For example, eels caught in freshwater as they migrated downstream have displayed otolith chemistry corresponding to saltwater residency (Jessop *et al.*, 2012). Indeed, in case of rapid movements, the otolith has not yet recorded the new environment and there is a discrepancy between capture site and otolith chemistry. Sr and Ba take around 15 days to be integrated and measured in juvenile eels (Yokouchi *et al.*, 2011).

Lipid analyses

Lipids are the main source of stored energy in migratory fish. In addition, lipids are involved in growth, reproduction, behaviour, vision, osmoregulation, thermal adaptation, and immune response processes in eels (Hirt-Chabbert and Young, 2012; Stottrup *et al.*, 2013). Of these lipids, fatty acids are commonly used as trophic biomarkers to explore feeding habits (Iverson *et al.*, 2002) and habitat use (Ackman, 1967) in a large variety of aquatic organisms, including eels (e.g. Prigge *et al.*, 2012; Ghazali *et al.*, 2013; Vasconi *et al.*, 2019).

Primary producers (e.g. photosynthetic algae), are the main *de novo* producers of essential medium- and long-chain (≥ 18 carbons) omega-3 and omega-6 fatty acids. Thus, these essential fatty acids are obtained by fish mostly through their diet. Although some fish species may have the ability to synthesize certain amounts of 20- and 22-carbon *n*-3 and *n*-6 fatty acids (e.g. eicosapentanoic acid, EPA = 20: 5*n*-3; docosahexaenoic acid, DHA = 22: 6*n*-3; and arachidonic acid, ARA = 20: 4*n*-6) from their 18-carbon precursors, marine fish seem to have lost this ability (or it is very limited), and hence must obtain these long-chain essential fatty acids “pre-formed” from their diet (Parrish, 2009). In general, ingested dietary fatty acids are incorporated into a consumer's tissues with little alteration, providing a basis for their use in tracking the flow of energy and nutrients across food webs (Iverson *et al.*, 2002). Importantly, it is possible to discriminate between marine and freshwater fish based on their fatty acid profiles (Parzanini *et al.*, 2020).

Fatty acid profiles of eel muscle tissue vary according to their diet and feeding habitat. The muscle of European eels captured from a lagoon in Italy had higher levels of *n*-6 fatty acids, e.g. ARA, compared to their marine counterparts (Vasconi *et al.*, 2019). In contrast, marine eel had higher levels of *n*-3 fatty acids, including EPA and DHA. The fatty acid composition of lagoon and marine eels was thus reflective of their feeding habitats, as well as of the intrinsic ability of lagoon vs. marine eels to synthesize certain fatty acids (Ghazali *et al.*, 2013; Vasconi *et al.*, 2019). Similarly, in Norway, marine and freshwater eels rely on two fundamentally different diets (Parzanini *et al.*, 2021a). The fatty acid composition of marine eel muscle was characterized by indicators of a marine-based diet (i.e. EPA, DHA, and *n*-3 fatty acids) and carnivory. In contrast, the muscle of freshwater eels contained the highest levels of *n*-6 fatty acids (i.e. ARA), reflective of freshwater ecosystems. This result, along with the information retrieved using lipid-corrected iso-

topic biomarkers, indicated that marine eels fed at higher trophic levels than their freshwater counterparts, perhaps due to a higher reliance on fish as prey items (Parzanini *et al.*, 2021b).

Fatty acid analysis reveals the recent feeding history of the fish, thereby complementing microchemistry analyses to yield a more comprehensive interpretation of individual migratory and habitat use patterns of eels. Lipids can also be sampled non-lethally from live eel using a muscle biopsy corer, which has no lasting effects on key individual fitness-related parameters, at least not in salmon (Bøe *et al.*, 2020). Such information is useful when eels are sampled in marine habitats and it is uncertain whether they are transient, recently migrated from freshwater or marine resident eels.

Stable isotope analyses

Stable carbon and nitrogen isotope ratios reflect long-term (years) dietary assimilation patterns (Fry, 2006). Carbon stable isotope ratios ($\delta^{13}\text{C}$) provide insight into the carbon sources from which consumers obtain their energy (Peterson and Fry, 1987), while nitrogen stable isotope ratios ($\delta^{15}\text{N}$) provide a continuous measure of consumer trophic position (DeNiro and Epstein, 1978), which may vary along with size, sex, and/or age (Fry, 2006). Stable isotopes have been used to describe community and trophic niche relationships (Vander Zanden *et al.*, 1999; Beaudoin *et al.*, 2001), habitat use (Power *et al.*, 2005; McMahon *et al.*, 2012), and intra-specific diet variability (Bearhop *et al.*, 2004), as well as to determine the effect of ecological perturbations on food web structure and function (Vander Zanden *et al.*, 1999; Ives *et al.*, 2013). Stable isotope analysis is also being used to describe the spatial scales at which organisms move during feeding (Rasmussen *et al.*, 2009), with the combined use of stable carbon, sulphur ($\delta^{35}\text{S}$), and nitrogen isotope ratios being particularly powerful for detecting differences in freshwater and marine habitat use or feeding (Doucet *et al.*, 1999). Increasing use of fin tissue sampling for stable isotope analysis of fish (Willis *et al.*, 2013) also means that it can be used non-lethally to understand eel ecology (Harrod *et al.*, 2005).

Despite the widespread use of stable isotope analysis, only a few studies have applied the method to elucidate feeding and habitat use in eels. These studies have collectively shown opportunistic and seasonal use of prey resources (Kaifu *et al.*, 2013), density-dependent feeding on freshwater macrobenthos (Dorner *et al.*, 2009), and linkages between head morphology and piscivory (Cucherousset *et al.*, 2011). A couple of studies have revealed variation in reliance on marine and terrestrial carbon sources within estuarine environments, suggestive of feeding plasticity in the use of freshwater and salt-water feeding habitats (Bardonnnet and Riera, 2005; Harrod *et al.*, 2005). Stable isotope analysis has also been used to cross-validate otolith microchemistry methods as a means of inferring seasonal freshwater–seawater migrations in American eels, providing evidence of movement where otolith microchemistry methods failed owing to limited otolith edge accretion (Clément *et al.*, 2014). Stable isotope analysis can be combined with fatty acid analysis to better understand the differences among prey resources and feeding habitats and, thereby, the advantages in terms of fitness and population-level consequences of feeding in each habitat (Iverson, 2009). In studies of European eel in Norway, the two approaches yielded largely consistent results (Parzanini *et al.*, 2021a).

Analyses of parasites

Parasite fauna and load have been used as biomarkers to understand fish host diet, migration, and population biology (Williams *et al.*, 1992; MacKenzie, 2002). Fish host parasite fauna may also be used in conjunction with other methodologies, such as stable isotope analysis, to reconstruct host fish diets more reliably than what can be achieved from stomach content alone (e.g. Locke *et al.*, 2013). The parasite repertoire carried by fish may reflect environments frequented in the past and earlier diets from when the host was at an earlier life stage. Many internal parasites (endoparasites) have complex, multi-host life cycles, with their transmission largely restricted to certain freshwater or marine habitats containing suitable hosts. Some parasites enter their fish host by penetration, whereas others as larvae in prey items via trophic transmission, establishing within host tissues as adults or as another juvenile stage (i.e. as definitive/final or intermediate hosts, respectively). Thus, knowledge of parasite life cycles can support inferences of past habitat use, migrations, and diets of fish (Williams *et al.*, 1992; MacKenzie, 2002; Marcogliese and Jacobson, 2015).

While in freshwater habitats, eels can acquire both micro- and macroparasites and even transient, short-term use of a given habitat by eels can be sufficient for infection. For example, eels in freshwater can become infected with a range of myxosporeans, and some of the tissue-invading species (e.g. *Myxobolus* spp.) may persist for years, indicating past freshwater residency in eels caught in the marine environment. Endoparasitic helminths (e.g. tapeworms, flukes, and nematodes) acquired in freshwater can also survive in marine resident eels, corroborating past freshwater residency. Some infections with larval stages, such as eye flukes (*Diplostomum* spp.), may be long-lasting (years) and particularly useful, while infections with gastrointestinal helminths may last a year or less (Chubb, 1979; Chubb, 1982) and thus shed light on more recent eel movements.

European eel can host at least 161 species of parasites (Jakob *et al.*, 2016), 34 of which are marine. Several marine parasite species infect only this host, which in itself represents strong evidence that marine residency has a long-standing history in eels. Most parasites acquired by eels in marine environments are helminths, especially adult or larval stages of trematodes (flukes), nematodes, and acanthocephalans, as well as some cestode (tapeworm) larvae (Koie, 1988; Kristmundsson and Helgason, 2007; Jakob *et al.*, 2016). Nearly all of these marine parasites are acquired by ingesting infected prey (intermediate hosts). Consequently, the life cycles of these parasites are generally restricted to certain marine environments where suitable intermediate hosts are found; however, it is important to understand specific parasite life cycles because these will vary among species, even of the same overall type (e.g. flukes). For example, some trematodes (e.g. *Deropristis inflata* and *Bucephalus fimbriatus*) are common in estuarine environments owing to the occurrence of a brackish-water gastropod that they require as their first intermediate host, while others (e.g. *Lecithochirium rufoviride*) mainly infect eels in full seawater environments because they use marine intermediate hosts. Such parasites can be good indicators of both short- (<1 year) and long-term habitat shifts, depending on the parasite species and life history stage. For instance, adult *Deropristis inflata* and larvae of marine nematodes (*Anisakis simplex*) have been found in large eels caught in rivers (Kennedy *et al.*, 1992; Aguilar *et al.*, 2005).

In a Norwegian study, the presence of a freshwater parasite in marine resident eel is considered evidence of incursions of eels into freshwater that were undetected by otolith microchemistry or fatty acid analyses (Haugland, 2020).

Although identification of parasites may require taxonomic expertise, the acquired information concerning past habitat shifts is unique. Often, the challenge with using parasites as biological indicators is the lack of knowledge about their particular life cycles, and their longevity in the host.

Blood transcriptome analyses

Since eels are critically endangered, it is important to develop non-lethal methods to determine physiological characteristics pertaining to their life histories. Currently, the most utilized methods (i.e. otolith microchemistry) require sacrificing the fish. Non-lethal measurements of variation in the blood transcriptomics can reveal the recent life history of eels (Bertolini *et al.*, 2022). Transcriptomic production is a crucial regulator of cell function, and intensity and the variability of expression of different genes in different tissues is strongly influenced by external factors and physiological status, together with individual variability (Connon *et al.*, 2018). For example, gene expression analyses for a limited number of key genes over controlled salinity changes have been successful in elucidating the molecular mechanism of salinity adaptation in eel larvae (Politis *et al.*, 2018; Politis *et al.*, 2021).

Advances in Next Generation Sequencing (NGS) technologies, in particular RNA-sequencing, allow to simultaneously profile the transcriptional activity of all genes in every living organism, thus accelerating the discovery of genes linked to specific physiological conditions. As non-mammalian vertebrates have nucleated, and thus transcriptionally active red blood cells, the blood transcriptome can be used as an indicator of the general metabolic and health status of the animal. The few studies so far available on blood transcriptomics in birds and fish have shown that changes in blood transcriptomes can be linked to chemical contaminant exposure and to urban vs. rural habitats (Watson *et al.*, 2017; Rodriguez-Jorquera *et al.*, 2019). RNA-sequencing represents a promising tool to perform untargeted and simultaneous profiling of the transcriptomic changes in the blood. More recently, transcriptomes from a blood sample were able to correctly classify 100% of freshwater and marine resident eels, and 83% of inter-habitat shifting eels using a minimum of 30 genes (Bertolini *et al.*, 2022). Collecting blood and determining salinity-habitat history during annual coastal eel monitoring surveys could provide the necessary information to quantify the proportion of marine resident eels and, to a lesser degree, inter-habitat shifting eels.

Use of electronic tags

The development of animal electronic tracking technology has provided unique tools for the study of animal behaviour both in aquatic and terrestrial habitats (Hussey *et al.*, 2015; Cooke *et al.*, 2022; Matley *et al.*, 2023). Electronic tags that can be used in fish research include radio and acoustic transmitters, data storage tags (also referred to as archival tags), pop-up satellite archival tags (PSAT; see Aarestrup *et al.*, 2009), and passive integrated transponder tags (PIT-tags) (Thorstad *et al.*, 2013). In telemetry studies, an electronic tag is attached or implanted into a fish, and information on position, movements, and/or measurements of environmental and physiolog-

ical parameters such as salinity, depth, and temperature thereafter recorded by stationary receivers or by active tracking. With good receiver coverage and high detection probabilities, telemetry can also be used to infer about the survival of tagged fish (Villegas-Rios *et al.*, 2020). Data storage tags record and store information on environmental and/or physiological parameters in the tag, and need to be retrieved to download the data. Electronic tags have been used in several studies on European eels in freshwater and marine habitats (Walker *et al.*, 2014; Westerberg and Sjöberg, 2015; Lennox *et al.*, 2018; Rohtla *et al.*, 2022), and can also be used to study migrations between marine and freshwater habitats (e.g. Aarestrup *et al.*, 2010). Acoustic telemetry provides outstanding information about fish behaviour but has the disadvantage of being relatively short-term when tagging smaller fish. Battery life of small transmitters (7–9 mm in diameter) usually limits the duration of observations to 1–2 years. This is sufficient to follow seasonal movements but inadequate to elucidate interhabitat movements that occur only once or twice during the lifetime of the long-lived European eel.

Conclusion

The decline of glass eel recruitment has been more pronounced, by a factor of 10, in the northern part of the eel's distributional range, including Norway and the Baltic countries compared to the southern part of their distribution (ICES, 2021). In several of these northern countries, a considerable proportion of the eel population occupies marine and brackish water habitats (Limburg *et al.*, 2003; Sjöberg *et al.*, 2017; Andersson *et al.*, 2019; Rohtla *et al.*, 2023). The higher prevalence of marine resident eels in the north can be explained by three main factors: (i) the higher productivity in the sea compared to freshwater at these higher latitudes; (ii) the potentially lower condition factor of glass eels as they recruit to continental habitats; and (iii) the lower river temperature at the time of upstream migration. Marine resident European eels are also common at the southern end of the geographical distribution—in Mediterranean and Atlantic lagoons and estuaries—where high temperatures and dried-out rivers may favour marine residency (Figure 1).

The abundance of marine resident eels is more challenging to assess than that of the catadromous freshwater contingent. Therefore, it is not accounted for in the overall population-level assessment (Figure 1). In fact, glass eel recruitment may be higher than evaluated if a significant proportion of eels settle and remain in coastal areas and skip the freshwater phase. Likewise, spawner escapement estimated from silver eel downstream migration may be lower than previously appreciated if some eels stop-over in coastal marine areas before finally migrating to their spawning area in the Sargasso Sea (Sjöberg *et al.*, 2017; Tambets *et al.*, 2021). Thus, the life strategy in terms of habitat choice shown by eel has important implications for the management and conservation of the species. A better understanding of habitat shifting and marine residency in eels would improve assessment of European eel populations.

It is currently unknown whether trends in the abundance of eel living in marine waters mirror the declines observed in freshwater. Resolving this issue will be important for future monitoring and management of the species (Righton *et al.*, 2021). While the reasons for the more pronounced population decline in the northern parts of the geographic distribution are

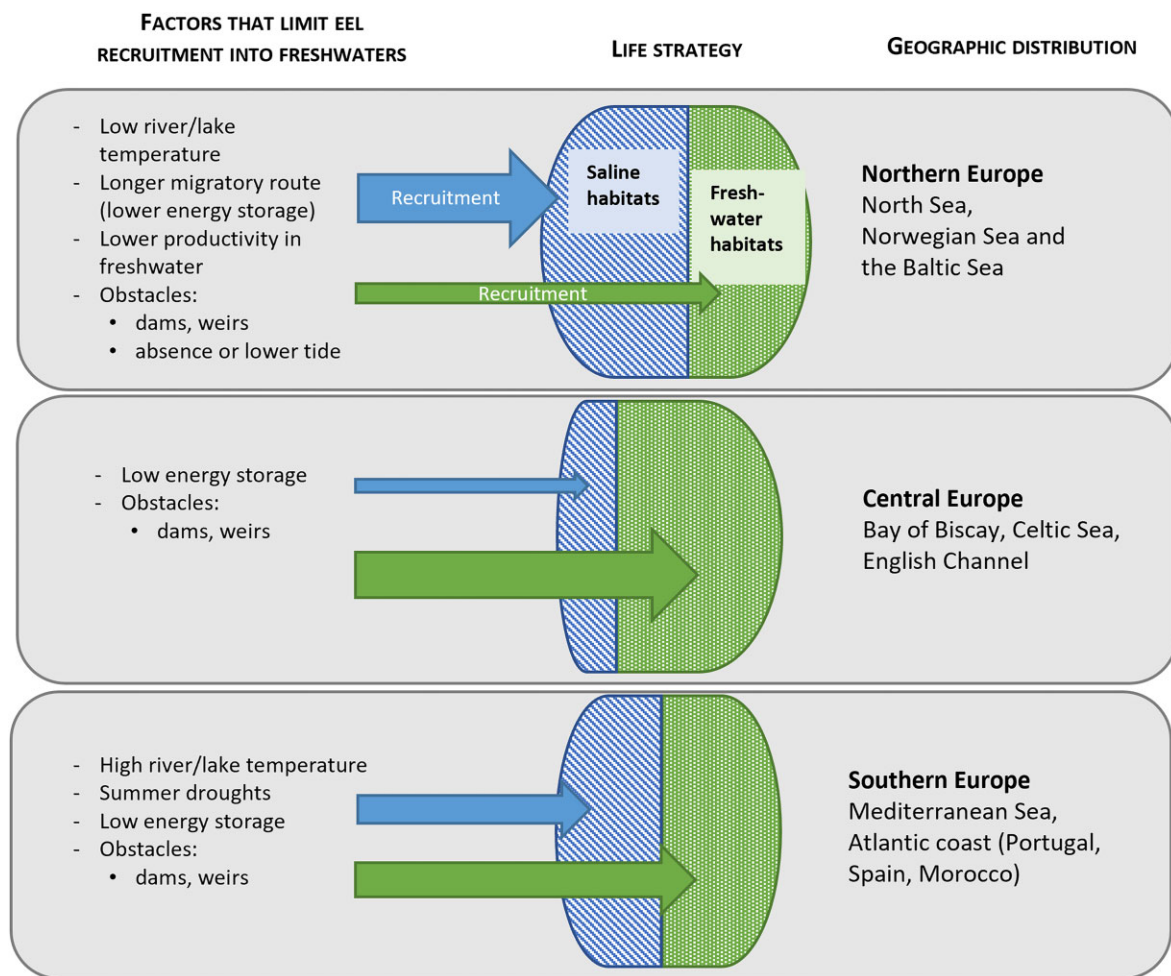


Figure 1. Facultative catadromy in the European eel. Limiting factors to upstream migration into freshwater result in general habitat loss. Arrows represent recruitment of glass eels or elvers into freshwater and saline (saltwater and brackish water) habitats (green and blue, respectively). The size of the arrows is proportional to recruitment. These proportions were estimated based on the number/importance of factors that limit recruitment into freshwater (on the left) and based on the authors' expert judgement. The current assessment of the European eel stock only considers freshwater recruitment (i.e. the green arrows).

largely unknown, it is possible that at least some of the declines observed in freshwater may be buffered by an increase in the proportion of eels displaying an alternate life strategy, such as marine residency. Knowledge of the magnitude of marine residency, therefore, is needed to obtain a reliable population estimate.

Skipping the freshwater phase may offer a clue to the resilience of anguillid eels. Marine eels represent a major component of eel intraspecific diversity—the genomic and phenotypic diversity found within the population—and, as such, contribute to the evolutionary strategy of the species. Outside the quantitative benefits of understanding the demographic importance of eels skipping the freshwater phase, qualitative knowledge may also have conservation value and may highlight the importance of habitat connectivity in coastal areas, estuaries, and wetlands. Human harvesting and habitat modification are the main drivers for defaunation of the marine ecosystem (McCauley *et al.*, 2015). Putative (increasing?) reliance on marine habitats for closing the life cycle of anguillid eels will have bearing on conservation planning.

Many of the factors that are thought to be responsible for the precipitous decline in the eel population are more

prevalent in freshwater systems. Hydroelectric power stations, cause considerable mortality in silver eels when they initiate spawning migration and move downstream in rivers. Many power stations are not equipped with fish passages for up- and downstream-migrating eels. Other freshwater threats, including pathogens, such as the invasive swimbladder parasite *Anguillicola crassus*, as well as the biomagnification and bioaccumulation of chemical pollutants probably hinder eel swimming and reproductive capacities (Pierron *et al.*, 2009). River fragmentation increases vulnerability to predators as individuals tend to aggregate in front of river obstacles (Guillerault *et al.*, 2015). Fishing pressure can be higher in the constrained riverine environment than it is in marine habitats, especially when targeting downstream migrating silver eels. As such, when glass eels delay their upstream migration into freshwater by more than a year, silver eel production may increase by two orders of magnitude (Jessop, 2000; Jessop *et al.*, 2002). Unfortunately, late upstream migrants are not routinely incorporated into population size estimates and models of eel life history, mortality, and production (Jessop *et al.*, 2002). Finally, wetlands, which constitute an important habitat for eels, have been greatly reduced since the 1970s. Many wetlands are now disconnected from the sea and estuaries. Polders, or tide weirs

restrict the presence of eels in such habitats where they used to be present in large numbers. Habitat loss has been identified as one of the reasons for the precipitous decline of *A. anguilla* (IPBES, 2018; ICES, 2020).

We need to improve our understanding of the ecology and life history of eels living in coastal marine environments, and to develop better tools to quantify the importance of marine habitats for eels. In particular, we need knowledge on their relative use of marine habitats to obtain reliable population estimates. For example, marine eels have a higher growth rate and mature at an earlier age (Daverat *et al.*, 2012; Rohdla *et al.*, 2023), which implies that they have a faster generational turnover, and contribute to the reproductive pool more quickly. If eels with different life-history tactics correspond to different genotypes (Pavey *et al.*, 2015), then marine residency has, and likely will, increase with the continued decline in the population, especially at higher latitudes.

More broadly speaking, investigating the importance of marine resident eels may yield insights into the behaviour of diadromous species in general, and how different life-history strategies may evolve with increasing temperature and population fluctuations. Global warming may affect the proportion of marine vs. freshwater residents by affecting the successful recruitment of larvae from the Sargasso Sea. The production of *Leptocephalus* larvae has been reduced (Westerberg *et al.*, 2018), but it is uncertain whether it will continue to decrease. The decline might be due to oceanic regime shifts, which have also reduced the production of marine snow, which is food for eel larvae (Knights, 2003; Miller *et al.*, 2016). The condition of eel larvae may also decrease due to temperature-driven increases in metabolism, as well as their temperature-dependent colonization of freshwater systems. However, an increase in river temperatures in northern areas may increase their propensity to migrate into freshwater. Combined, these scenarios suggest increasing use of marine habitats as a plastic response to increasingly variable freshwater environments that may represent relatively poor habitats for eels. Conversely, perhaps we are only belatedly appreciating an unrecognized but nonetheless common, occurrence of marine resident eels and are also simply observing an alternate tactic exhibited by this species. Considering the long-standing traditional coastal fishery for yellow eel (Aker and Koop, 1979; Dekker, 2003; Ojaveer *et al.*, 2007), the latter seems likely. Thus, it is of paramount importance that we increase our knowledge of eel habitat use and movements in marine habitats. This will allow us to better evaluate the current population status and to develop appropriate mitigation and conservation strategies for sustaining eel populations, improving their resilience in the face of global warming.

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CMFD, ABS, and HIB conceived the ideas. All authors contributed to the original draft, reviewed, and edited the manuscript.

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Data availability

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