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The Blueprint of the European Eel Life Cycle: Does Life-History Strategy Undermine or Provide Hope for Population Recovery?

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ABSTRACT

The life cycle of the European eel (*Anguilla anguilla*) is inherently risky because it relies on the successful migration of larvae and adults across thousands of kilometres of the Atlantic Ocean. In between these migrations, eels need to grow and develop to maximise their potential for successful reproduction. Eels have a number of life-history characteristics at each life stage that minimise mortality, starvation and predation risks and maximise opportunities for growth. In the larval and silver eel phases, eels select specific habitats and adopt efficient swimming behaviours to minimise predation and migration failure risks. In the glass and yellow eel phase, the opposite is the case, and plasticity and adaptability enable occupation of a broad ecological niche that maximises growth opportunities and enables a continent-wide distribution. Under natural conditions, these characteristics enable enough individuals to survive, grow and reproduce so that the population is resilient to natural risks. However, there is increasing evidence of impacts of anthropogenic activities that eels may be particularly sensitive to, resulting in a declining population with reduced resilience. Climate-linked oceanic risk factors are likely to have a significant influence on the recruitment of eels but are not well understood and cannot be easily modified. However, interventions to mitigate known impacts in the growth environment offer hope for population recovery. A greater understanding of the plasticity of the growth phase and the impacts of risks during the oceanic phase is essential to enable management interventions in the Anthropocene to be fully effective.

1 | Introduction

In 1912, the Danish eel scientist Johannes Schmidt stated in his landmark Nature paper on the location of the spawning area for European eels (*Anguilla anguilla*) that "the whole story of the eel and its spawning has come to read almost like a romance, wherein reality has far exceeded the dreams of fantasy" (Schmidt 1912). This narrative of the eel life cycle being fantastical, or a mystery, was a theme that Schmidt (and others: e.g. Grassi 1897; Tucker 1959; Dekker and Casselman 2014) often used in his scientific work (Schmidt 1923a, 1923b) and was fitting at a time when the broad parameters of the eel life cycle were still being discovered. Although we know much more about eel biology today, it is still possible to experience this sense of wonder (Fort 2002; Svensson 2020), because the ecological challenges that eels overcome at all life stages are a

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Etymology of Ghoti: George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

rich catalogue that integrates marine, estuarine and freshwater environments (Tesch 2003; Righton et al. 2021), and the 'unobservable' or cryptic nature of the marine phases maintains this element of mystery. However, given the significant population decline of the European eel, it is no surprise that the species (and the genus in general) has also become emblematic as a keystone species associated with the five key risks of global change in the Anthropocene epoch: climate change, habitat fragmentation and loss, pollution, introduction of non-native species and overexploitation (Dekker and Casselman 2014; Bevacqua et al. 2015; Drouineau et al. 2018).

2 | The Concept of a Design Plan or "Blueprint"

In the introduction to their classic text book 'Fisheries Ecology', Hart and Pitcher (1982) explained that their approach was to take a deliberately "broad view of the subject, including a consideration of fish as elements in a delicately balanced ecosystem, and features of their adaptive physiology and behaviour", which led to an opening chapter on "Fish Design Plans". In our view, the concept of these design plans or "blueprints" explain how different aspects of a species' biology and life history help to reduce the risks and threats that individuals will face within their natural environment, and how their adaptations maximise the chances for successful reproduction and continuation of the individual's genetic line. However, in the Anthropocene, some natural threats to eels are amplified by new and additional risks caused by human activities. Given the scale of these new risks, it is worth revisiting the blueprint of the European eel in the context of historical ecology (i.e., the evolutionary response to the ecological challenge), before integrating and comparing this with the threats of the Anthropocene (i.e., the existential threat to population integrity).

3 | The Life Cycle of the European Eel

Anguillid eels evolved between 70 million and 40 million years ago from a tropical deep-sea ancestor (Aoyama et al. 2001). From the first moments of life, a European eel faces a remarkable ontogenetic and geographic journey. Transparent 'leaf-like' larvae, called leptocephali, hatch from eggs fertilised in the Sargasso Sea. European eel leptocephali are found throughout the northern Atlantic Ocean and within the Mediterranean Sea (Grassi 1897; Miller et al. 2015; Figure 1), with their size increasing as they move further away from the spawning area. Leptocephali arrive annually at the coastal slope (typically defined as the 200 m contour at the western edge of Europe) between June and September and metamorphose into glass eels (Schmidt 1909; Tesch 2003). These migrate inland towards the coast and estuaries, where they aggregate into large schools and rapidly colonise the available brackish and freshwater habitat in the lower reaches of rivers before moving further upstream and occupying almost all accessible habitats. Although many eels return to or never even leave the marine environment during their growth phase as yellow eels, the majority are thought to migrate into and remain in river catchments for most of the remainder of their lives (Righton et al. 2021). Given the large area over which leptocephali are distributed by drift, and the tenacity and ability of glass eels to colonise freshwater, brackish and even marine habitats, the growth phase of the European eel, the yellow eel, is found and thrives in most of the river systems in Europe (including the brackish inland seas the Baltic and the Black Sea), as well as some rivers in Northern Africa and Asia that drain into the Atlantic and Mediterranean. This gives the European eel one of the broadest geographic and habitat distributions of any freshwater fish[1] (Tesch 2003; Righton et al. 2021; Figure 1). Yellow eels can spend between five and over 20 years (and sometimes much more; Dekker et al. 1998; Andrews et al. 2025) in the growth phase before they migrate back to the spawning area in the Sargasso Sea. This is particularly pronounced for females, which tend to be older and bigger than males when they undergo a final 'silvering' metamorphosis that prepares them for the spawning migration. Silvering encompasses a range of physiological pre-adaptations as well as changes to physical appearance, the most notable of which are the enlarged eyes and silver colouration of the ventral surface (Acou et al. 2005). Silver eels typically migrate downstream in the autumn and winter months and then disappear into the ocean (Schmidt 1923b; Briand et al. 2020). Knowledge of silver eel ecology in the ocean has been increasing in recent years by virtue of tagging and tracking studies (Righton et al. 2016; Wright et al. 2022) but the final reproductive acts of the silver eel's life have only ever been evidenced by the capture of the very smallest leptocephali larvae in the Sargasso Sea (2015) and hormone-induced artificial reproduction in captivity (Freese et al. 2017).

Of the five temperate species, European eels exhibit some of the most extreme characteristics of their type: by far the longest (distance and duration) oceanic migrations and the largest latitudinal distribution (Righton et al. 2021). Compared to most other species of temperate fish species, almost everything about each stage of the life cycle is extreme. As for all anguillids, the persistence of the species is underpinned by surplus production of larvae (Jellyman 2021). However, the resilience of the life cycle is also critically enabled by the way that eels are able to mitigate the many natural risks to which they are exposed through physiological, physical, behavioural and ecological adaptations. This adaptability enables individuals to survive in a wide range of conditions and environments (Daverat et al. 2006; Parzanini et al. 2021; Arai et al. 2019) and thus for the panmictic population to persist despite such significant challenges.

4 | The Eel Blueprint in the Anthropocene: A Time of Global Change and Challenge

With the onset of the Anthropocene (Waters et al. 2016), eels are currently faced with exposure to multiple, and likely cumulative, anthropogenic stressors or impacts over a long lifetime (Jacoby et al. 2015; Drouineau et al. 2018; Bourillon et al. 2022), and the natural resilience of the eel life history may, perversely, switch to a state of exceptional vulnerability, which pivots on the existence of a single spawning site in the Sargasso Sea, and to which the success at each life stage is linked. To assess and integrate these risks and vulnerabilities, it is necessary to break down the life history into each of the main stages and assess

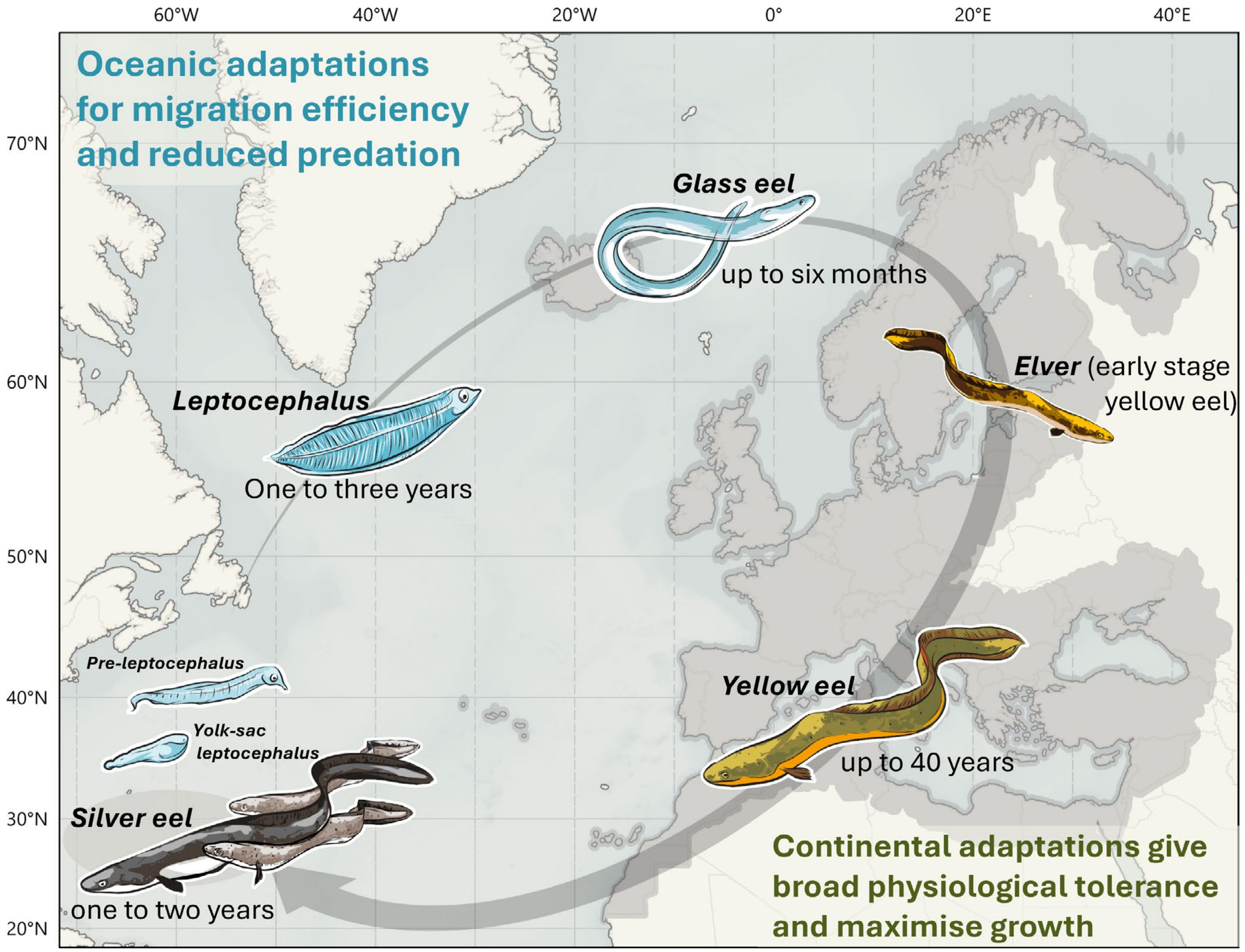

FIGURE 1 | The distribution and life cycle of the European eel. The oceanic phase is characterised by energy minimisation and anti-predator adaptations, while the continental phase is characterised by physiological tolerance/flexibility and growth maximisation. The grey shading on the European continent shows the extent of the distribution in the growth phase (downloaded from https://www.iucnredlist.org/species/60344/152845178), while the grey ellipse in the Atlantic Ocean shows the approximated spawning area. Drawings of eel life stages are adapted with permission from Het Nieuwsblad (12/01/2022).

both the adaptations that each stage relies upon and how the anthropogenic risks act upon them.

4.1 | Stage 1—The Trans-Atlantic Migration of the Leptocephalus Larvae to the European Continental Shelf

After hatching in the Sargasso Sea, the main purpose of leptocephalus larvae is to maximise migration success to the continental shelf. The open ocean is a very dynamic environment and, for larval fish, a highly risky one. Leptocephali possess a number of striking adaptations (Table 1). For example, they lack haemoglobin and pigment (Miller et al. 2015), making them almost completely transparent and virtually invisible to predators, but the most notable feature of the leptocephalus stage (shared with other species that have leptocephalus larvae) is their exceptional length, which may reach up to 100 mm or more (Schmidt 1923a; Miller et al. 2015), and the distance covered and duration that they remain in the larval form which, at up to two or three years and thousands of kilometres, is arguably one of the longest teleost larval phases known (Kuroki et al. 2014). These features are effectively what enabled Schmidt (1912) to plan surveys to map the occurrence and density of leptocephali in the Atlantic Ocean and to identify the Sargasso Sea as the breeding area (Schmidt 1923a).

The large size of the leptocephalus larvae of European eels may also be an adaptation to the relatively unique ecological niche created by the oligotrophic conditions in the Sargasso Sea and wider Atlantic. In this habitat, pico- and nanoplankton dominate but, due to their size, are not a suitable food source for typical fish larvae. Their large size allows leptocephali to 'leapfrog' the size gap in the trophic chain by targeting aggregations of primary producers, such as larvacean houses or low-quality but ubiquitous and continuously produced marine snow (e.g., Westerberg 1990; Mochioka and Iwamizu 1996; Miller 2009; Miller, Marohn, et al. 2019; Miller, Westerberg, et al. 2019) that descends from surface waters. By doing so, the leptocephali are effectively adopting a top- or large-predator strategy within the generally low

TABLE 1 | Life stages, the notable adaptations of that phase, the natural risk that the adaptation mitigates, the benefits of the adaptation and the anthropogenic risk that either negates the effectiveness of the adaptation or adds to the risk.

Stage (goal)	Significant feature	Natural risk	Benefit	Anthropogenic risk
Leptocephalus (*trans-Atlantic migration*)	Extended duration	Starvation, predation	Flexibility and resilience in migration duration	Climate-induced warming of the ocean increases the starvation risk
	Large size	Increased energetic demand	Feed on larger prey items at higher trophic levels, predator refuge	Climate-induced warming of the ocean increases starvation risk
	Transparent	Reduced oxygen delivery efficiency (no haemoglobin)	Predator avoidance	
	Buoyant	Location of leptocephali in the water column makes them available to predators that occupy surface to 300 m depth	Reduces swimming cost	
	Forage on marine snow	Low nutritional content of food requires continuous feeding	Ubiquitous food source	Microplastic pollution in oceans reduces energy intake, introduces potentially toxic metabolites and diseases
	Migration driven by drift	Failed migration, unpredictable immediate environment	Reduces swimming cost	Climate-induced warming of the ocean increases starvation risk and changes current patterns
Glass eel (*colonisation*)	Transparent		Predator avoidance	
	Aggregates	Shoals attract pelagic and benthic predators	Individual predation risk is reduced, migration success increases	Fisheries exploit aggregative nature
	Osmotic flexibility	Physiological stress and costs	High environmental tolerance	
	Sensitive to tidal, water flow, olfactory cues	Navigation and colonisation failure	Increased orientation capability	Barriers increase delay to up-river migration and predation risk

(Continues)

TABLE 1 | (Continued)

Stage (goal)	Significant feature	Natural risk	Benefit	Anthropogenic risk
Yellow (*growing*)	Up-river migration	Density dependent sex determination may over-skew sex ratios	Large habitat area to occupy increases growth opportunities	Full access to river systems is blocked by barriers to migration
	Trophic plasticity	Can become trapped in low-quality habitats	Generalist feeding behaviour	Exposure and ingestion of a wide range of contaminants from catchments and prey
	Full pigmentation	Visible to top predators	Camouflage for a benthic life style	
	Benthic behaviour		Hiding in the substrate helps avoid predators	Exposure to contaminants in substrates, and exploited by fishers
	Long-life with stalled maturation	Potential for mismatch between escapement timing, duration of spawning migration and spawning season	Resistant to environmental changes	Bioaccumulation of toxins, only one opportunity to spawn
	Tolerance of poor environments	Low growth rates, physiological stress	Broad habitat occupation	Exposure to contaminants, entrapment due to migration barriers
	Ubiquity within river catchments		Broad habitat occupation	Target for fisheries, exposure to catchment-wide threats
Silver (*trans-Atlantic migration and reproduction*)	High fat content	Reserves are not sufficient, whichleads to starvation/exhaustion	Efficient fuel	Bioaccumulation and release, reduction in river productivity, spawning or migration failure, targeted by fishers
	Stomach atrophy	Reserves are not sufficient, which leads to starvation/exhaustion	No energy is wasted to maintain the digestive system or to look for food	
	Buoyancy control using a swim bladder	Energy required to maintain buoyancy using gas exchange is considerable	Swimming depth regulation with reduced swimming effort	*Anguillicola crassus* impacts on buoyancy control and swimming efficiency
	Responsive to flow	Navigation and orientation failure. Timing of migration partly dependent on higher river flow during the autumn and winter season	Swimming direction with the water flow direction	Entrained in hydropower, easy to target with fishing pressure

(Continues)

TABLE 1 | (Continued)

Stage (goal)	Significant feature	Natural risk	Benefit	Anthropogenic risk
	Responsive to darkness/ nocturnal	Restricts timing of movement, slows down escapement	Predator avoidance	Artificial light may disrupt migration and increase predation risk
	Tidal stream migration/ selective tidal stream transport	Restricts timing of migration	Bio-energetic efficient movement	
	Occupation of mesopelagic depths	High pressure at depth modifies physiological and cellular processes	Predation refuge	
	Diel vertical migration	Unknown, but has energetic cost & physiological impact from the transition between extreme environments	Unknown, but may be linked to maturation, navigation	
	Flexible migration duration	Mismatch in arrival time at the spawning grounds	Increasing likelihood of finding conspecifics at the spawning grounds	Climate change increases metabolic costs of migration and barriers to migration delay onset of migration
	Reversible silvering	Delay and re-silvering may reduce energy reserves and impact spawning success	Minimises risk of delay or disruption to migration	
	Oceanic spawning in Sargasso Sea	Navigation and migration to continental growth habitat a risk to resulting larvae	Oligotrophic ocean has few predators, so reduces the impacts of predation of larvae	Climate change has impacted the productivity of Sargasso Sea with impacts on larval survival
	Extreme swimming efficiency	Requires trade-offs in other aspects of physiology and anatomy	Maximises energy for reproduction	Climate change increases the metabolic costs of migration

trophic level of the plankton community, finding competitive release from smaller plankton yet still consuming sufficient energy through their prey to maintain their large size and activity, akin to the planktivorous sharks (Gore et al. 2023). Leptocephali are able to sustain their large size because they contain a relatively low proportion of respiring tissue, coupled with a high proportion of buoyant gelatinous tissue (Miller 2009), thereby minimising metabolic rate. This large size presumably favours successful recruitment when they arrive at the continental slope, perhaps because this reduces the threat posed by the diversity of potential predators in coastal waters (Miller and Tsukamoto 2020).

In the Anthropocene, changes in ocean climate and circulation, coupled with widespread microplastic pollution (Table 1) are likely to amplify the natural risks that leptocephali face when navigating the ocean. For example, it is generally accepted that a significant proportion of leptocephali naturally become trapped or entrained in currents that are not on a direct route to the coast of Europe. The flexibility to have an extended leptocephalus phase is a bet-hedging strategy that increases the probability of (re)-entrainment into the North Atlantic drift (Bonhommeau et al. 2008; Bonhommeau et al. 2010). Well-documented and measured changes in oceanographic conditions resulting from anthropogenic climate change may lead to the increased probability of delay or the duration of migration due to changes in the rate or patterns of ocean circulation (Friedland et al. 2007; Pacariz et al. 2014) or increase starvation risks due to the impact of higher water temperatures on basal metabolic rate (Westerberg et al. 2018), assuming food intake cannot increase to compensate. These starvation risks may be compounded by the increased risk of feeding on increasingly prevalent microplastic pollution (Kvale et al. 2020) which may reduce overall energy uptake and impact physiological pathways. Furthermore, because lipophilic contaminants stored by yellow eels during their continental growth phase may be incorporated into reproductive products, the ability of newly hatched larvae to tolerate thermal and physiological stressors may be reduced and therefore increase mortality rates (Bourillon et al. 2020).

The potential for anthropogenic impacts on the leptocephalus stage may be significant, but it is also highly uncertain (Table 1; Figure 2) because of the difficulties of conducting large-scale,

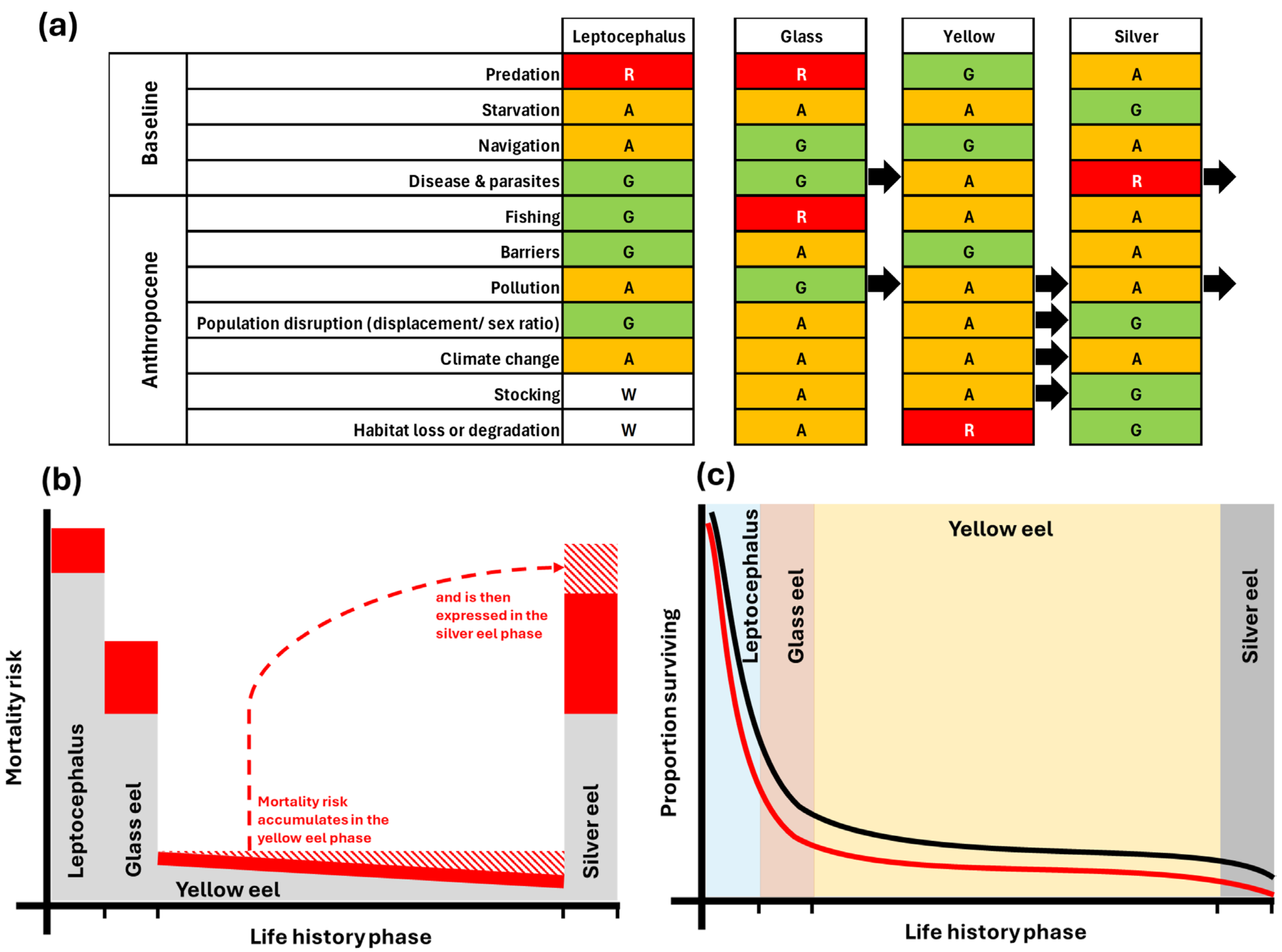

FIGURE 2 | Concepts of the European eel life cycle showing risks at each life stage, either as the baseline or as those in the Anthropocene. (a) relative red, amber and green (RAG) rating of risks at each life stage and in different epochs, as judged by the authors. Risks that accumulate in one stage, but which may affect mortality at the next stage are shown by arrows; (b) comparison of the risk profile in different epochs: Baseline mortality risk is shown in grey, while the additional risks that occur in the Anthropocene are shown in red; (c) comparison of survivorship in an unimpacted system (black line) and in the Anthropocene (red line). Survivorship at each life stage may not be sufficient to ensure population sustainability because the proportion escaping to spawn is below the spawning stock biomass threshold to generate surplus production.

long-term oceanographic studies to generate reliable estimates of leptocephali abundance in any part of their geographic range. On one hand, the additional risks may be relatively trivial compared to the general natural mortality risk, which has typically been estimated in modelling studies at an annual rate of between 95% and almost 100% (Pacariz et al. 2014). On the other hand, even small changes in mortality rate at the leptocephalus stage will propagate through the life cycle and affect the population size when silver eels return to the Sargasso Sea to spawn. Given the low state of the population, recovery and restoration require substantial increases in recruitment to the growth phase. Thus, even though the additional anthropogenic mortality risks may be relatively trivial compared to the general natural mortality risk, anthropogenic impacts on the larval phase make population recovery all the more difficult. It is therefore important to consider the likelihood of a higher long-term oceanic mortality rate to avoid undermining efforts to protect the production of later life stages.

Clearly, due to their large scale and the extended feedback loop of human impacts on the ocean, mitigating actions beyond those already identified in significant global commitments on biodiversity, climate and marine litter (Convention on Biological Diversity 2022; United Nations Framework Convention on Climate Change 2015; United Nations Environment Programme 2022) are unlikely to be extended significantly. Instead, mitigating actions could instead be developed that act upon later life stages, i.e., by adapting eel management plans to account for increased uncertainty in larval production and therefore requiring less reliance on future substantial increases in recruitment to achieve management targets. In tandem, further research to gain insight into whether any increase in the mortality rate caused by anthropogenic factors could be absorbed by surplus production would be valuable and help to parameterise life-cycle models more accurately.

4.2 | Stage 2—Colonisation of the Coastal and Freshwater Habitat by Glass Eels

Leptocephali metamorphose into glass eels (transparency is retained, but individuals develop the commonly recognised anguilliform shape, anatomy and movement) when they reach the continental shelf (Schmidt 1909), and they migrate towards suitable coastal, brackish or freshwater growing habitats. To navigate, glass eels primarily use olfactory, temperature and tidal cues (Deelder 1958; McCleave and Kleckner 1982; Sola 1995; Righton et al. 2021) but other cues, e.g. sonic or magnetic, are also likely to be important (Durif et al. 2013; Cresci 2020). Either because these cues bring them together, or because they also seek out conspecifics (Briand et al. 2002), glass eels accumulate in huge numbers at the coast, aided in part by the use of selective tidal stream transport. The survival or success rate of glass eels arriving at the coast after their metamorphosis from the leptocephalus stage is poorly understood (Cresci 2020) and is likely to vary considerably over time and between different areas or times of year. The greatest natural risk to survival during this phase is predation (Table 1; Figure 2), given the abundance of potential predators that inhabit estuaries and the lower reaches of rivers, either fish such as seabass (*Dicentrarchus labrax*) and pike perch (*Sander lucioperca*; Cresci 2020; Griffioen et al. 2022), or a wide range of bird species. However, since glass eels are relatively large at metamorphosis (~6 to 8 cm, Tesch 2003), compared to other larval fish, and are transparent, their vulnerability is likely reduced compared to other prey items that predators may encounter. Furthermore, since glass eels occur in large shoals, the predation risk to an individual is reduced by this 'predator swamping' mechanism (Pitcher et al. 1998).

In the Anthropocene, glass eels face significant additional risks to their survival as well as having their natural risks amplified by human activities. Based on standardised time-series that have been collected at selected monitoring sites in river estuaries in the North Sea, the number of glass eels has declined to approximately 0.6% of the 1960–1979 average, and along the rest of the European Atlantic coast, the observed decline is to approximately 5.5% of the historic average (ICES 2022a). Although some of the reduction is likely to be the consequence of impacts upon leptocephali, a significant proportion may relate to increased mortality at the glass eel stage. Historically, because their aggregative behaviour ensures high catch per unit effort (CPUE), the greatest anthropogenic risk was from fishing mortality, which has been estimated in the past at up to 40% (and potentially more) of recruitment in some catchments (Drouineau et al. 2018). However, following the introduction of eel management plans that were strongly focussed on reducing fishing mortality (ICES 2013), other anthropogenic risks have attracted attention, such as modified water flows (Bouchard et al. 2022), entrainment into water intakes (Beaulaton and Briand 2007) and migration barriers such as weirs, sluices, shipping locks, water pumping stations and hydropower plants. For example, it is estimated that there are about one million fish migration barriers in European waterways (Belletti et al. 2020), which prevent glass eels from colonising freshwater areas from the sea (Mouton et al. 2011). Furthermore, because glass eels become delayed while they accumulate downstream of the barriers, the relative risk from natural predators and potential starvation is increased (Griffioen et al. 2022, 2024) and may make glass eels more available to fisheries or increase the duration that they experience the physiological stress of occupying water of varying salinity (Tesch 2003). Notably, the loss of historical wetlands has reduced the availability of suitable habitat and therefore the carrying capacity (Kettle et al. 2011; Šmejkal et al. 2025), which reduces population resilience. The threat from declining oxygenation of coastal waters as a consequence of climate change (Breitburg et al. 2018), or the increasing prevalence of marine heat waves (Capotondi et al. 2024), may also pose a risk to glass eel survival.

Given the threats that human activities pose, it is inescapable that anthropogenic impacts significantly increase mortality risk at the glass eel stage and that any surplus production will be significantly reduced by the time glass eels occupy the growth habitat (Figure 2c). As for the leptocephalus stage, any increase or reduction in mortality at the glass eel stage will propagate through to later life stages. Measures to reduce the mortality risks due to human impacts are diverse, and many are in active use or development (Cutts et al. 2024). However, the effectiveness of these measures is not always fully understood or monitored, and therefore their potential for contributing to population recovery is difficult to forecast. While limiting fishing activity on glass eels is a quantifiable reduction in pressure, the benefits or impacts of engineered or nature-based solutions for offsetting the impacts of habitat loss or damage caused by barriers to migration are less well understood and need further research. This also applies to understanding the benefits of one well-used and historically applied method to increase eel densities, that of glass eel translocation and stocking (Righton et al. 2021) that are difficult to determine (Dekker and Beaulaton 2016), and may vary between locations. Furthermore, any measures that allow for the capture and transport of live glass eels could also undermine conservation efforts due to the incentives created for trafficking and illegal fishing/trade (Alonso and van Uhm 2023; Stein et al. 2025). Improving measures to reduce demand for glass eels (i.e., supply side controls), or to increase the pace at which full life-cycle aquaculture solutions can be implemented, would help to reduce mortality risks at the glass eel stage.

4.3 | Stage 3—Occupation of Growth Habitat by Yellow Eels to Reach an Effective Body Size for Reproduction

Following the risky journey from the Sargasso Sea to the growth habitat, eels become pigmented and change into the 'yellow eel' form. The main goal of this stage is to occupy a relatively low-risk habitat and grow large enough to mature. Due to the differing requirements for investment in reproductive tissue at the silver stage, the strategy for males and females differs slightly. Males appear to adopt a time-minimisation strategy so as to return to the ocean and reproduce as quickly as possible, while females appear to adopt a size-maximisation strategy and remain in the growth habitat for as long as necessary to reach a suitable size and fat content (Vøllestad 1988; Larsson et al. 1990). This gives rise to a sexual dimorphism, but both strategies are underpinned by the same adaptive mechanisms: plasticity of habitat choice and foraging behaviour.

This plasticity applies to a number of aspects: growth duration, habitat choice, sex determination and foraging behaviour. The yellow eel stage is also tolerant of a wide range of critical environmental conditions, such as salinity, water temperature and oxygen level. This plasticity is almost the opposite of the larval and silver phases, in the sense that yellow eels are not adapted to finding very specific habitats to minimise risk, but rather that they are adapted to the broadest range of habitats available to maximise growth opportunities. Consequently, the plastic behaviour of the yellow eel life stage is essential to effectively reach the goal of maturing as fast as possible with minimum risks of failure. It allows them to colonise whichever habitat they first arrive at but enables them to take advantage of opportunities to move to more favourable habitats or to minimise the impact of periods of sub-optimal conditions. Yellow eels therefore occupy a huge variety of habitats including coastal habitats, tidal marshes, rivers, small tributaries and streams, but also lentic systems such as ponds and lakes when they are (periodically) connected to a river[2] (Tesch 2003). Because eels do not need to partition energy into reproductive effort until the silver stage, all the surplus energy derived from feeding can be channelled into somatic growth (Tesch 2003). In many habitats, eels take their place amongst the top predators within that habitat, feeding opportunistically on a range of prey, including other fishes (Lammens and Visser 1989; Van Liefferinge et al. 2012). This has the consequence that eels are more resilient to annual changes in the productivity of their growth habitat than would otherwise be the case and has ensured the survival of the population over geological time-scales despite the significant ecological challenges of drought and ice ages (Kettle et al. 2011). Critically, however, because the rate of growth can vary enormously depending on the varying productivity of different habitats, the age at which eels migrate back to the sea can also vary enormously, spanning a few years to several decades (Svedang et al. 1996; Durif et al. 2020).

In the Anthropocene, despite the dispersion of the population across a very large geographic range, anthropogenic impacts are also widely dispersed, and therefore few eels will escape the impacts of modification, degradation, pollution of habitat, climate change or population manipulation (Jacoby et al. 2015). For example, large-scale catchment modification may prevent eels from moving freely across a river's catchment, compromising their ability to move between habitats to maximise foraging opportunities (Van Liefferinge et al. 2012) or affecting the density-dependent sex ratio (Crowley et al. 2022). Climate change appears to act in a number of different ways, from increasing the risk of mortality due to drought or reducing the ability of individuals to move to more favourable habitat due to changes in river flow or hydrodynamics. A critical influence of climate is likely to be mediated through changes to the length of the foraging season, leading to faster growth and therefore earlier escapement, which could have a pronounced impact on population dynamics. Finally, the longevity of the yellow phase, the association with benthic habitats and the reliance on benthic food sources means that exposure to non-lethal but chronic and persistent pollutants is higher than for many other fish species, making eels at risk of bioaccumulation of toxins (Geeraerts and Belpaire 2010).

While the plasticity of the yellow phase ensures that individuals are able to survive these widespread and non-lethal impacts, they seem likely to have an impact on population viability by either reducing their reproductive fitness in advance of silvering (Bourillon et al. 2020, 2022) or increasing the mortality risk in the silver phase (Geeraerts and Belpaire 2010; Figure 2c). Thus, these non-lethal impacts on the yellow eel population combine with the reduction in carrying capacity caused by habitat loss and the significant risk of reduced recruitment at earlier life stages caused by the combined effects of climate change, fishing mortality and barriers to migration. The evidence available strongly supports that habitat quality and availability for European eel is degraded compared to the pre-Anthropocene (Jacoby et al. 2015; Clavero and Hermoso 2015).

Although it is a particular challenge to incorporate the scale of anthropogenic impacts and their spatial variability into management models, sufficient evidence exists to suggest how to intervene to reverse them. For example, a number of measures have illustrated how to enable eels access to growing habitats such as fish passes, including specific eel passes or eel gutters, and adjusted tidal barrier management (e.g., setting tidal gates ajar when the sea level is higher than the adjacent freshwater, allowing glass and yellow eels to migrate inland, or providing eel 'ladders'; Mouton et al. 2011; Van Wichelen et al. 2021; Watz et al. 2019). In terms of downstream migration, studies have shown that shutting down hydropower turbines during the eel migration season can stimulate a safe passage to the sea (Eyler et al. 2016). Also, innovative systems at water pumping stations or different types of pumping regimes are being developed to increase the success and survival of passing eels (Bruneel et al. 2024; Evans et al. 2024). However, providing effective solutions for downstream passage is still in its infancy and requires further research. For instance, shipping locks can be a substantial migration barrier for eels; yet, no solutions have been proposed for these barrier types in shipping canals (Vergeynst et al. 2021; Verhelst et al. 2018). The effective implementation of such mitigations requires a coordinated approach to ensure that the benefits of one measure are not negated by others at a different location in space and/or time. Eel Management Plans (EMPs) should provide for such coordination of protective measures.

While controls on fishing effort were a primary focus during the early phase of eel management plans stemming from the European Union's Eel Regulation (EC1100/2007; EU 2007), finding ways to increase habitat suitability or reduce levels of pollution would be a valuable next step. However, developing methods that can identify the habitats that should be prioritised for restoration or remediation is a necessary first step in a strategy to mitigate the impacts of habitat degradation on yellow eels. These should be coupled with existing efforts to identify the most effective ways to reduce the impacts of the very diverse types of barriers to migration or sources of pollution (EU 2007). In the same way that it is important to put in place mitigations to reduce glass eel mortality, developing robust indicators to determine the effectiveness of these actions will be critical to optimising and adapting habitat management plans that will provide a foundation for population recovery.

4.4 | Stage 4—Trans-Atlantic Migration by Silver Eels to the Spawning Area

In the final part of the life cycle, eels return to the 'oceanic strategy' of the larval phase. The migration is one-way; eels only spawn once in their lifetime, so any migratory strategy has to maximise an individual's chances for success and minimise the risks. While semelparity coupled with an extremely long growth phase is an unusual life-cycle strategy (and one that frustrated many scientists attempting to identify how eels reproduced, beginning with Aristotle in 350 BC 1902), as detailed in the previous section, it (if necessary) provides the flexibility for eels to attain or exceed the size and condition required for them to return successfully to the Sargasso Sea and spawn. This strategy is not unique to European eels but is also observed in all other species of anguillid eels.

The adaptations to achieve the ocean migration effectively are much different from the leptocephalus phase because silver eels have to actively travel back to their place of origin and use a number of physical, behavioural and physiological adaptations to do so. Aside from their obvious streamlined shape, silver eels use downstream currents in rivers and tidal currents in estuarine and coastal seas to reduce transport costs (Vøllestad et al. 1986; Jansen et al. 2007; Verhelst et al. 2023). When traversing ocean waters, which may take more than 12 months (Righton et al. 2016; Wright et al. 2022), silver eels spend most of their time in deep, and therefore cool, strata, which appears to reduce the cost of transport by reducing metabolic rate. While this may have a significant impact upon the effective function of muscle and nervous tissues (Righton et al. 2012), it appears to enable lower costs of transport (Pohlmann et al. 2023) and is clearly under selective pressure (all European eels ever observed in the ocean, and indeed all anguillids, move into deep and cold water habitats during their spawning migration; Righton et al. 2021).

Predator avoidance in the silver eel stage appears to be achieved through behavioural mechanisms, such as nocturnal behaviour (in rivers and in shallow seas; Verhelst et al. 2023) and selection of deep habitats in the ocean (Righton et al. 2016). The silvering process itself is a pre-adaptation to oceanic migration, with the counter-shading colouration acting to reduce detection and the enlargement of the eyes to enable light detection when occupying deep, extremely low light environments (Acou et al. 2005). Furthermore, the cessation of feeding (which leads to or is caused by stomach atrophy) removes the need to spend time searching for food (thereby reducing the need to move into strata of the ocean with greater predation risk) and is likely linked to other adaptations, such as the efficient use of fat and other types of metabolite as fuel (van Ginneken and Maes 2005; Chow et al. 2010), and the physiological or metabolic adaptations to spending time at high hydrostatic pressure (Righton et al. 2012). Not feeding during the oceanic migration also means that eels have to gather more energy stores in freshwater than, for example, an ocean-migrating juvenile salmon.

In the Anthropocene, many of the additional threats that silver eels encounter are either literally upstream of the ocean or occur in the life stages prior to the silvering process (which could be considered 'temporally upstream'). In the literal sense, silver eels can experience barriers to migration before they reach the ocean, delaying their departure. While the timing of departure of silver eels appears to be flexible during an 'autumnal period' that can extend to more than 6 months in some locations (Briand et al. 2020; Verhelst et al. 2025), the consequence of delay or disruption may act to deplete valuable energy reserves and reduce reproductive output (Verhelst et al. 2018) or perhaps increase the likelihood of reversal of the silvering process (Sjöberg et al. 2017). Furthermore, interaction with barriers such as hydropower plants increases the direct (turbine damage) and indirect risks to mortality (reduced energy stores, increased predation) and fishing mortality remains a risk. In the temporal sense, silver eels are exposed to threats that accumulate in the growth phase but are only expressed once the ocean migration starts. These include stored persistent pollutants being mobilised into the blood or accumulating to increasingly toxic levels within diminishing reserves (Geeraerts and Belpaire 2010; Belpaire et al. 2016), insufficient or poor quality fat content stored at the yellow stage causing migration or reproductive failure (Belpaire et al. 2016; Palstra et al. 2006), and the threat of dormant pathogens or parasites such as EVEX or *Anguillicola crassus* contracted in freshwater causing mortality or impacts during the migration (van Ginneken et al. 2005; Palstra et al. 2007, and summarised in Table 1; Figure 2). Finally, the impact of climate change on the seawater temperatures that eels experience may increase the metabolic cost of migration, directly impacting migration success or the amount of reserves available for spawning (Righton et al. 2021).

Many of the threats at the silver eel stage, until they migrate beyond the boundaries of freshwater and transitional Eel Management Units associated with EMPs, are implicitly and explicitly accounted for in life-cycle models that are used to set escapement targets. These targets are designed to mitigate effectively against migration failure because they provide the sufficient leeway required to enable a large enough proportion of the silver eel population to escape to the ocean such that, despite the risks of spawning and recruitment failure, or direct and indirect mortality, reproductive potential will enable population recovery in the future. The EU Eel Regulation currently requires that the biomass of escaping silver eel be at least 40% of that which would be expected under pristine conditions, i.e. if no anthropogenic influences had impacted the population (EU 2007). However, there are still many unknowns about the spawning ecology of European eels (Wright et al. 2022), including whether the current population size provides enough spawning eels to avoid depensatory effects. Future research to improve understanding of spawning ecology, effective population size and the risks of depensation (e.g., Rowe et al. 2004; Möllmann et al. 2021) is necessary to ensure that escapement targets can achieve a putative spawning target. Until that knowledge is available, there is some encouraging progress reported for some catchments, with recent estimates of current escapement up to 74% of pristine biomass (ICES 2022b). However, escapement is lower than this 40% target in many others, and there is as yet no clear trend for population recovery despite most EMP targets being in place since 2010. In consequence, the latest scientific advice is to prohibit all fishing mortality (ICES 2024) and couple this measure to other conservation efforts to increase population production and resilience.

5 | The Impacts of Cumulative Risks to Eel Populations

Jellyman (2021) identified that the critical feature of Anguillid life history, in terms of their almost universal success in temperate and tropical environments, is strongly linked to surplus production of larvae. Through the production of vast numbers of offspring, eel populations are, of course, resilient to fluctuations in natural mortality. However, he also noted that with the declining glass eel recruitment across the majority of species and the large number of barriers to upstream migration, density-dependent processes are strongly affected, with a consequent impact on the production of large female eels, increasing the risk of future low recruitment.

Our view offers a complementary perspective, compatible with, but emphasising different aspects of the eel life history and setting these in the context of the wide range of threats that eels face. In essence, our thesis is that the "blueprint" makes European eels uniquely adapted to the dynamics and chance events of their ecosystems, but also makes them exceptionally vulnerable to anthropogenic risks that occur (i) directly at each life stage (such as fishing and migration barriers impacting the glass, yellow and silver stages), (ii) through the accumulation of risk factors (predominantly in the yellow eel phase) that have an impact later in life (predominantly in the silver phase) or (iii) through changes to global climate that impact all life stages (and perhaps the leptocephalus stage in particular). Unlike other freshwater or marine species that are impacted by one or two main or localised anthropogenic threats (e.g., Atlantic bluefin tuna that is affected mostly by fishing pressure), which can be addressed locally or regionally through management intervention, the distribution of European eels maps across almost all types of threats (Jacoby et al. 2015; Drouineau et al. 2018; Righton et al. 2021) and the life-cycle maps across multiple, cumulative threats, including climate change, fishing pressure and pollution (Figure 2b). In consequence, the proportion of the population expected to survive the life cycle in the Anthropocene continues to reduce for each life stage and overall (Figure 2c), thereby increasing the challenge of achieving silver eel escapement targets and population recovery.

6 | Is There Hope for the Future of Eels?

The European eel population has expanded and contracted over geological time (Kettle et al. 2011) and, given the resilience of individuals and local stocks, the threat of total extinction seems unlikely. However, the European eel is considered critically endangered, and the assessed population remains at a historic low (ICES 2022a). This is without taking into account the phenomenon of shifting baselines, which likely means that our current assessment is uninformed by the state of the population more than 100 years ago (Pauly 1995). What then, given the many threats of the Anthropocene, is the future of eels?

An important aspect to resolve in asking this question is whether the population of the European eel has moved beyond a tipping point for recovery (e.g., Möllmann et al. 2021), or whether its life-history traits will enable a path to recovery. Our discussion highlights how the plasticity and resilience of European eels are key features of their ecological success in the growth habitat, and these same traits are effective responses (sensu Dakos 2018) against many of the impacts in this phase of the life cycle. Critical questions remain as to some of the aspects of the life cycle, and particularly the impacts of e.g. climate and pollution on the oceanic phases (Righton et al. 2021). These are difficult to assess directly, and so uncertainty in predictive population modelling will remain.

Clearly, designing and implementing conservation measures that will be effective for the European eel in the managed environment, as well as identifying and prioritising those that have sufficient return on investment, is critical. However, evidence for the most effective interventions is relatively sparse (Cutts et al. 2024) and can be difficult to discern due to the plasticity of eel life-history traits (Bevacqua et al. 2015). Furthermore, the differences in drivers of mortality risk at different life-history stages present a large range of potential interventions to choose from, and the differing level of relative mortality risk between different life-history stages creates uncertainty for decision-makers. For example, it could be argued that reducing mortality risk at the glass eel stage would have the greatest impact on population recovery because each percentage point reduction acts upon a much larger population than at the yellow or silver eel stages and would have a greater benefit than reducing mortality by a percentage point at the later life stages. Conversely, since natural mortality is also very high at the glass eel stage, the relative benefit per individual is lower, and the counter-argument that efforts to protect individuals at the silver eel stage are more important has merit. Given the year-to-year variability in annual recruitment (ICES 2024) and the uncertainty in the stock-recruitment relationship (Åström and Dekker 2007), the potential benefits of focusing on one life stage or another are difficult to assess. Much like the eel blueprint appears to take a 'hedging' approach to risk, the best management strategy for population recovery may well be to adopt a precautionary approach and to hedge against this uncertainty by taking action across a broad range of interventions at all life stages. This is similar to the management dilemmas that need to be taken under the 'deep uncertainty' identified for Atlantic cod (*Gadus morhua*, Conradt et al. 2024). For European eels, the most effective interventions include habitat restoration, mitigating migration barriers and pollution and reducing fishing mortality (Jacoby et al. 2015). These and other measures are identified in the European Eel Regulation (EU 2007) and are projected to reduce pressure on the population and increase the escapement of spawners. However, coordinating an international management approach and maintaining conservation momentum over the time scale of decades over which this will act may prove difficult (Dekker 2016), particularly given the complex jurisdictional landscape that the EU Eel Regulation, as well as other eel management regulations (such as the General Fisheries Control Measures in the Mediterranean) rests over. Moreover, the response of the eel population to these measures is somewhat difficult to predict (ICES 2022b), so ongoing research (e.g., oceanic factors) and the development of better modelling approaches that integrate deep uncertainty into management plans (in the way described by Conradt et al. 2024) will be necessary.

Despite the challenge that European eel recovery presents, there is ample and encouraging evidence that shows how concerted action can lead to the recovery of aquatic species and habitats. For example, after decades classified as endangered, populations of several species of tuna have improved in status thanks to internationally coordinated management actions (IUCN 2021), and the Pacific salmon complex now has clear pathways to recovery even if they are difficult to implement (Chalifour et al. 2022). Despite the difficulties of integrating multiple management measures that target different habitats and life-history stages and although the blueprint for the European eel may contain vulnerabilities to the challenges of the Anthropocene, it also contains many resilient features that, under the right conditions, may enable the population to survive and bounce back. The effective and continued management of fishing pressures, the removal of barriers to migration and the design of integrated, local solutions appear the most likely pathways to mitigating human impacts (Cutts et al. 2024), but only if they are coupled with monitoring plans to determine the effects of these interventions. By doing so, the most effective measures will be identified and refined and by continually developing and improving assessment and management methods, the chances of effective and sustained population recovery of European eels will be increased.

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Conflicts of Interest

The authors declare no conflicts of interest.

Endnotes

[1] It could be argued that if eels did not already occupy much of the European continent and North Africa, their ecological characteristics are in some ways very similar to successful non-native species—they can adapt to a wide range of environmental conditions, have a very broad carnivorous diet, and are remarkably resilient to environmental stressors that would thwart many other species of native fish.

[2] European eels are sometimes found in land-locked water bodies that are artificially stocked, noting that their occurrence in these habitats is a management action rather than a natural state.

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