Anguillid eels

Michael J. Williamson[1, 2*], Charlotte Pike[3], Matthew Gollock[3], David M. P. Jacoby[4], and Adam T. Piper[1, 2]

[1]Institute of Zoology, Zoological Society of London, Outer Circle, Regent's Park, London, NW1 4RY, UK

[2]Department of Genetics, Evolution and Environment, University College London, Darwin Building, 99-105 Gower Street, London, WC1E 6BT, UK

[3]Conservation and Policy, Zoological Society of London, Outer Circle, Regent's Park, London, NW1 4RY, UK

[4]Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

* Correspondence: Michael J. Williamson, michael.williamson@ioz.ac.uk.

Summary

Anguillid eels have fascinated humans for centuries, but many gaps still exist in our knowledge of these mysterious species. There are 19 species/subspecies of the genus *Anguilla*, which are found globally, with the exception of the eastern Pacific and southern Atlantic. Despite being known as freshwater eels, this is a misnomer - all anguillids are facultatively catadromous, born in marine environments, developing in continental waters, with a proportion never entering freshwater at all. Anguillid eels have several life history traits that have allowed them to exploit a broad range of habitats. As such, anguillid eels play an important ecological role in both marine and freshwater environments as well as being a commercially valuable species. As a consequence of this, anguillid eel populations are under threat from multiple stressors, including barriers to migration, pollution, parasites and disease, climate change and unsustainable exploitation. Six species are listed in a Threatened category on the International Union for Conservation Nature (IUCN) Red List of Threatened Species, and four are listed as Data Deficient. Strengthening conservation and management of these species is essential for national and international action, and further research provides an exciting opportunity to develop a greater understanding of this mysterious genus.

Main text

Anguillid eels and human culture

The enigma surrounding anguillid eels has fascinated humans for hundreds of years, and even today aspects of their behaviour and ecology remain shrouded in mystery. Aristotle once thought they grew out of mud and humid ground, while others suggested that they regenerated from the skins of old eels, dew, slime or horsehair. Anguillid eels have been traded and consumed by humans for centuries. In medieval England eels were so abundant that they were used to pay rent before there was enough available coinage. In mid 19th century Japan, a road was built specifically to transport live eels 250 km from Lake Nakaumi in Izumo Province to Osaka. The exploitation of anguillid eels continues today, driven by significant economic and culturally important markets. Consumption of eels is important culturally across many countries. In Japan, where eels hold significant cultural affiliations, the festival Do-yo no ushi no hi (Day of the Ox) signifies the start of the summer and is celebrated by eating kabayaki (grilled eel). In addition to consumption, eels have cultural ties for many indigenous communities across the globe; linked to folklore, art, literature, legend and belief. Native Māori, North American and Australian aboriginal cultures pay respect and express awe towards eels. Certain Buddhist sects in Japan do not consume eels, as they believe they are messengers of the Buddhist saint. Images of eels across these cultures display a diversity of legends where eels are shown favourably or unfavourably, with respect or distaste. Understanding the cultural and historic significance of eels provides important context for their conservation.

Anguillid eel diversity

Anguillid eels evolved more than 50 million years ago and have survived a succession of ice ages and continental drift. This demonstrates their evolutionary robustness and remarkable adaptive capacity. There are 19 species and sub-species within the family Anguillidae (Table 1). They are globally distributed and inhabit fresh, brackish and coastal waters of more than 150 different countries (Figure 1). The Indo-Pacific Ocean is considered as the origin of speciation in anguillid eels and based on molecular phylogenetic studies, with *A. borneensis* and *A. mossambica* believed to be the most probable ancestral species. Spawning areas have been discovered/proposed for many anguillid species (Figure 1). Known spawning areas are based mainly on larval catches, and estimated spawning areas are based on other additional information, including, evidence about population structure, tagging studies of silver eels, or species ranges in relation to ocean current patterns

Table 1 List of the 19 species/subspecies of anguillid eels, organized in order of species complex. Subspecies are not assessed under the IUCN Red List Categories and Criteria, and status therefore refers only to the species level (marked by[a]). Source: Ayoama (2009), Hsu et al., (2020), Righton et al., (2021). Maximum length (L_{max} cm), where known, is given and taken from Righton et al., (2021). Dorsal colouration is taken from Hsu et al., (2020).

Latin name	**Distribution**	**Dorsal colouration**	**L_{max} cm**	**IUCN status**
A. celebesensis	Tropical	Mottled	150	Data Deficient
A. interioris	Tropical	Mottled	80	Data Deficient
A. megastoma	Tropical	Mottled	165	Data Deficient
A. luzonensis	Tropical	Mottled	100	Vulnerable
A. bengalensis bengalensis	Tropical	Mottled	200	Near Threatened[a]
A. bengalensis labiata	Tropical	Mottled	175	Near Threatened[a]
A. marmorata	Tropical	Mottled	200	Least Concern
A. reinhardtii	Tropical	Mottled	165	Least Concern
A. borneensis	Tropical	Bi-coloured	Not known	Vulnerable
A. japonica	Subtropical/ temperate	Bi-coloured	150	Endangered
A. rostrata	Subtropical/ temperate	Bi-coloured	152	Endangered
A. anguilla	Temperate	Bi-coloured	133	Critically Endangered
A. dieffenbachii	Temperate	Bi-coloured	185	Endangered

A. mossambica	Tropical	Bi-coloured	150	Near Threatened
A. bicolor bicolor	Tropical	Bi-coloured	80	Near Threatened[a]
A. bicolor pacifica	Tropical	Bi-coloured	123	Near Threatened[a]
A. obscura	Tropical	Bi-coloured	110	Data deficient
A. australis australis	Subtropical/ temperate	Bi-coloured	130	Near Threatened[a]
A. australis schmidtii	Subtropical/ temperate	Bi-coloured	130	Near Threatened[a]

72

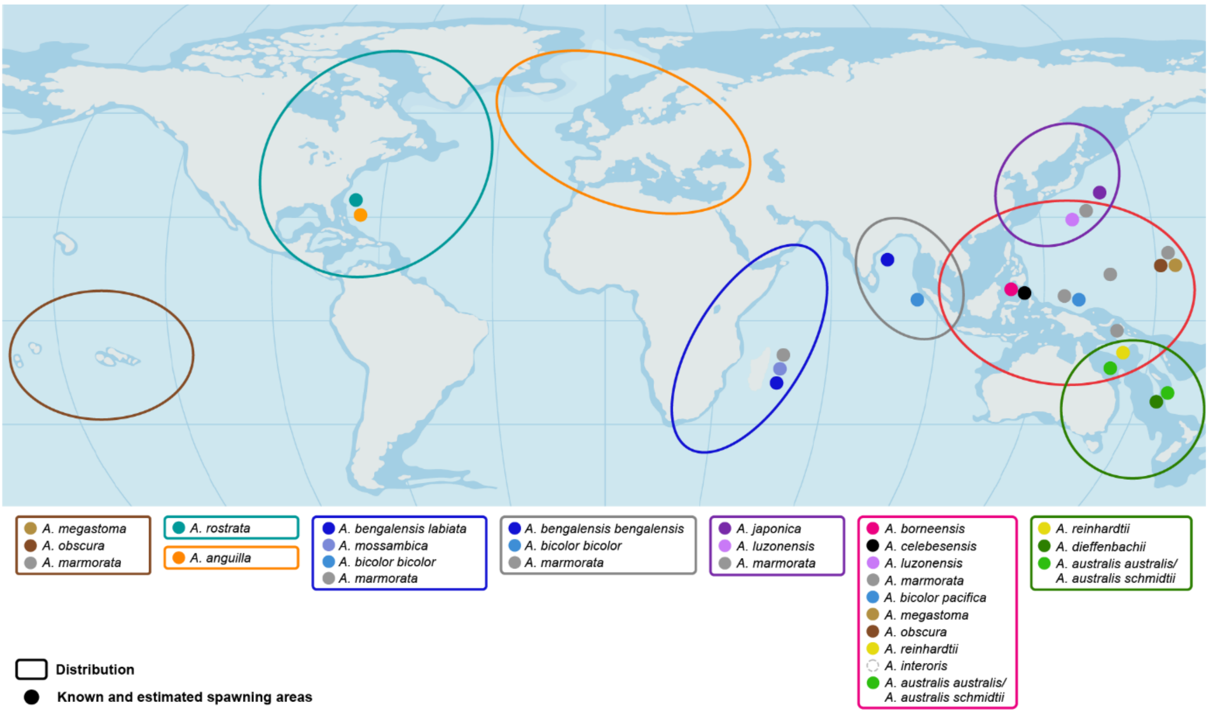

Figure 1 Map of global distribution and known and estimated spawning areas of the 19 species and sub species of anguillid eels adapted from Arai (2020) and Righton et al., (2021). Distributions are indicated by coloured ellipsoids, and spawning areas by coloured filled circles. Note that some species (e.g., *A. marmorata*) may have several regional distributions and spawning areas and as such may appear more than once on the map.

Anguillid eels – a unique life history

Anguillid eels have a complex and unusual life cycle. All anguillid eels are semelparous and catadromous. This means they breed in a single spawning event in the open ocean, where the eggs hatch, and larvae (lepocephali) migrate towards continental waters to feed and grow, before returning to breed (Figure 2). The marine spawning phase is believed to be essential for the completion of the life cycle posing a significant challenge for anguillid conservation. Spawning populations have been shown to be comprised of mixed age cohorts, where latitude and density are thought to play an important role in determining age and size at maturity. Most eel species are believed to be panmictic, with all mature individuals mating randomly at the same place and time. However, unlike other anguillids, *A. marmorata* and *A. bicolor* are thought to have multiple spawning sites, in the Indian and Pacific Oceans respectively (Figure 1).

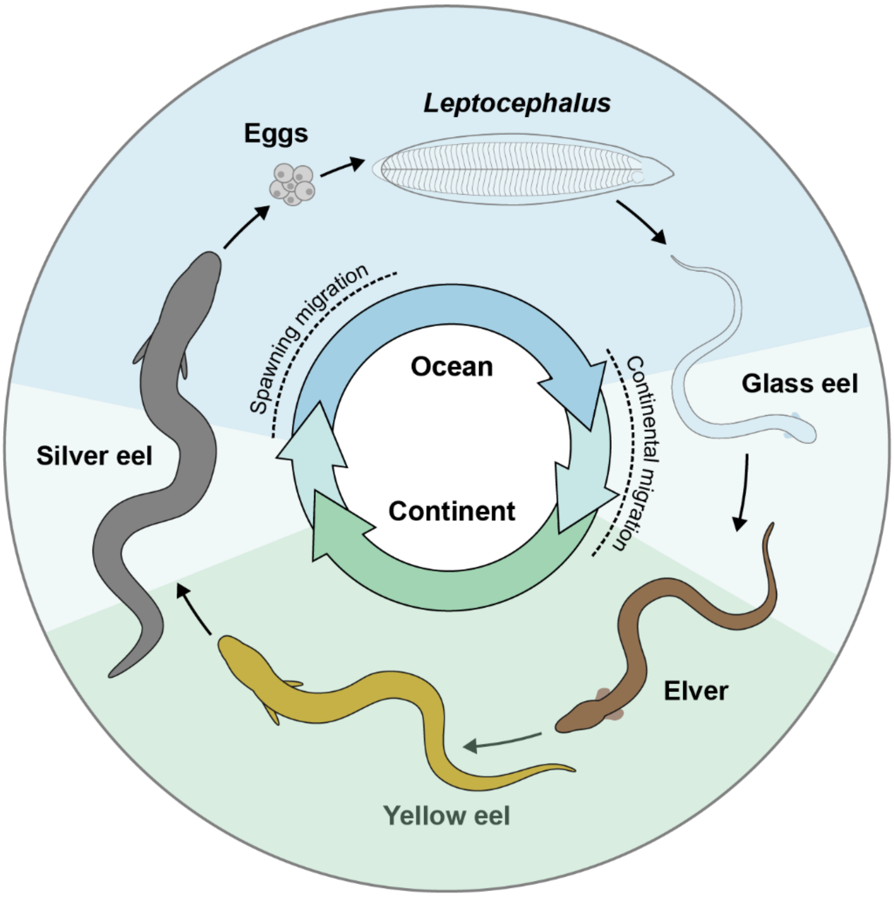

Figure 2 The catadromous life cycle of an anguillid eel.

94

It is important to note that there is considerable variation in life history traits, such as migration distance, developmental habitat type, growth rate and age at maturation between and within anguillid eel species. However, there are a number of phases in an eels life that have specific morphological characteristics and which are common across all anguillids. After hatching, the marine larval leptocephalus stage is leaf-shaped and very different from the elongate shape most associated with anguillids (Figure 2). During migration the leptocephali grow and elongate to become transparent glass eels (Figure2, Figure 3) upon arrival at the continental shelf. Glass eels migrate into coastal marine habitats such as estuaries and lagoons, and freshwater systems, such as rivers and lakes, where they feed, grow and develop. Historically it was thought that anguillid eels were freshwater obligates, but they are now known to be to be facultatively catadromous with a proportion of the population spending some or all of their growth phase in saline systems. As the glass eels grow and pigment they become elvers and then yellow eels; these are morphologically similar, distinguished primarily on size, with a counter-shade of yellow / brown / green dorsum and lighter ventrum (Figure 3). The final stage is the marine-migratory silver eel, which will ultimately mature to breed. This phase is characterised by a darkened dorsum, silvery counter-shading, and the development of large eyes, all adaptations for the marine environment (Figure 3). Following ‘silvering’ these maturing eels migrate from continental growth habitats to open ocean to breed just once before dying.

Figure 3 The continental life stages of anguillid eels; glass eel (top); elver (second); yellow eel (third); silver eel (bottom). (Photos: Chris Grzesiok (glass eel, elver), David Curnick (yellow eel), Adam Piper (silver eel)).

Anguillid eels, like other broadcast spawning fish, are highly fecund. Fecundity in eels is positively related to fish size, and females adopt a size-maximising strategy. Eels rely on high fat reserves for this egg production, as well as for fuel for migration. Sex determination in anguillid eels is plastic, and, unusually, predominantly a response to growth rates and population density, with high density favouring development of males, and lower density favouring females. Hence sex ratios typically change along the length of a waterway, with males predominating in lower reaches where densities tend to be higher but the proportion of females increasing with increasing distance.

Anguillid eels - additional biology and ecology

Anguillid eels are characterised by a slender, elongated body, notable pectoral fins, and emphasised caudal fin, with other fins absent, reduced or fused with the caudal fin. Anguillid eels can be separated according to morphological features e.g., bi-coloured/mottled dorsal colouration or short/long dorsal fin but also in relation to their geographies e.g., tropical/temperate or Northern/Southern hemisphere (Table 1). In most species, male eels grow faster than the females, and the latter generally achieve a greater age and size at sexual maturity. Eel growth rate increases with temperature and is generally faster in saline water than fresh. There are ontogenetic differences in preferred habitats with small individuals preferring areas of shallow water and fine substrates but with increasing size eels prefer greater depth. As well as these ontogenetic differences, habitat preferences may also vary between species and populations. Anguillid eels are found in a range of habitats from small streams to large rivers and lakes, and in estuaries, lagoons and coastal waters and are closely associated with the availability of daytime cover, which can include tree roots, macrophytes and anthropogenic material such as pipes and debris. During migrations anguillid eels are found in open ocean habitat. However, they are rarely seen in this environment, and how they utilise open ocean habitats is not fully understood.

Ecologically, eels are important opportunistic predators and scavengers. Anguillid eels are omnivorous, with crepuscular and nocturnal foraging patterns, and, as with habitat, diet is linked with body size, as well as ontogenetic preferences. Smaller individuals feed on bivalves, amphipods, shrimp and polychaete worms, with larger eels consuming larger prey such as fish and crustaceans. They may even forage widely on terrestrial prey like insects and earthworms during periods of increased water levels which allow them to enter newly submerged areas. Eels are typically ambush predators and have different feeding mechanisms ranging from suction feeding to grasping and tearing using rotational spinning. Their acute olfactory sensitivity enables them to locate prey with precision. Typically, eels do not feed every day, and can go long periods without feeding. For instance, *A. anguilla* have been tracked undertaking their spawning migration, a non-feeding stage of their life cycle, for over 18 months and unfed eels kept in captivity have survived for up to five years. Anguillid eels are also important prey species in the diet of a range of predators including larger eels, sharks, birds, and aquatic mammals, such as otters and seals.

Anguillid eels are robust, hardy and resilient fishes, and frequently survive in conditions that other species cannot tolerate. They often inhabit areas with poor water quality, survive droughts and, as mentioned above, can survive extended periods of fasting. Even temperate species display remarkable tolerance to varying temperatures. *A. rostrata* can survive under ice-covered water, below the freezing point of fish tissue, by using mud substrate as a thermal refuge. Some species may also burrow into moist mud during loss of surface water enabling them to survive drought conditions. Eel haemoglobin has a high affinity for oxygen and eels can undergo periodic apnoea, meaning they can tolerate oxygen-depleted waters, where other species cannot. Eels also have an exceptional tolerance to elevated CO2 levels in the blood, conditions associated from warm temperatures and/or eutrophication. Eels employ a buccal pump system whereby the opercular chamber allows eels to respire while being immobile and so they can remain motionless for extended periods. Further, they can augment gill respiration with cutaneous respiration, enabling them to breathe air at the surface. The widespread distribution of anguillid eels is most likely a result of their adaptability and physical and behavioural plasticity, enabling them to utilise a wide range of environments and habitats.

Migration and movement

Anguillid eels move with a sinusoidal swimming action which is energetically conservative and efficient for long distance travel. They also take advantage of passive transport from oceanic, tidal and river currents. Leptocephali are largely carried along by ocean currents, while glass eels use selective tidal transport to enter rivers and migrate upstream. Following movement into continental waters, anguillid eels generally have a more sedentary mode of life as they develop. Anguillids also have the ability to climb, particularly as juveniles. This allows juvenile eels to negotiate many types of natural and engineered river structures such as waterfalls, dams and weirs, and they can also travel through subterranean aquifers and enter coral atolls via subsurface outfalls. When movements along water bodies are impeded, anguillid eels may even crawl out of the water and over vegetation to continue their upstream or downstream passage.

There are species-specific variation in oceanic migrations across anguillid eel species, from less than one hundred to thousands of kilometres. For temperate species, distances from spawning areas to continental habitats are typically longer than for tropical species. *A. anguilla*, migrations are estimated to range from 5000–10,000 km. The scale of spawning migrations of tropical species varies considerably with some species undertaking migrations between 1000–3000 km. The spawning ground for *A. celebesensis*, a tropical species, could be as little as 100 km from continental habitat. Anguillid eels exhibit diel vertical migrations on their route to the spawning ground, occupying deeper depths in the lower mesopelagic layer (500–700 m) during the day and moving to the shallower waters in the upper mesopelagic layer (100–300 m) at night.

Prior to the oceanic spawning migration, temperate anguillid species in river systems typically undergo a seasonal downstream migration which is associated with decreases in temperature and day length and increased water level and flow velocity and discharge. In tropical anguillid eels the period of downstream migration extends throughout the year, which results in year-round spawning and recruitment to continental habitats.

Threats to anguillid eels

As anguillid eels inhabit a wide range of habitats and ecosystems they can serve as indicator, umbrella and flagship species for conservation of aquatic biodiversity. However, many anguillid eel species have undergone a dramatic decline in only a few decades. Of the recognised 19 species and sub-species, six are listed in Threatened categories (Vulnerable, Endangered, Critically Endangered) on the IUCN Red List of Threatened Species. This could be greater with four of the tropical species listed as Data Deficient, where there is not enough information to be assigned a category. The three most economically important species are listed as either Critically Endangered (*A. anguilla*) or Endangered (*A. rostrata, A. japonica*). These declines have been driven by a number of threats, such as climate change; pollution; barriers to migration; unsustainable exploitation; and disease and parasites.

Climate change has altered both oceanic and continental water conditions, through alterations in ocean temperatures and currents, and increased droughts and flooding, which impact continental and spawning migrations. These changes are occurring at scales that are challenging to manage. Increased pollution levels in marine and freshwater ecosystems can have significant negative impacts on anguillid eels, which are particularly vulnerable to contamination due to their high trophic level and reliance on lipids as a fuel for migration. Measures such as the European Water Framework Directive aim to improve water quality for aquatic species and ecosystems, which should reduce pollution in our systems, but the success of these types of legislative measures can be variable. By 2015, only 53 % of waterbodies across the EU were achieving 'good' ecological status, and was as low as 17% in countries, such as the UK.

Fragmentation resulting from the construction of riverine barriers (e.g., weirs and dams) have particularly detrimental impacts on eels. This is mainly through reducing access to growth habitat, altering distributions, restricting migrations, increasing energy costs, as well as direct mortality and sublethal injuries through encountering turbines and water pumps or impingement on hard structures such as screens. To increase connectivity and reduce impact of barriers, mechanisms have been added to exclude eels from harmful areas, such as intakes, and guide them to safe downstream passage routes using physical (e.g., screens, guiding walls and passes/fish lifts) or behavioural (e.g., hydraulic, light, acoustic) measures. Unfortunately, there is no single technique that can be universally applied, and efficiency of applied systems remains low.

Unlike most commercially important fish species that are usually harvested as adults, eels are exploited by recreational and commercial fisheries at all continental life stages i.e., glass eels, elvers, yellow eels and silver eels, for both consumption and aquaculture. As temperate eel populations have declined, increased exploitation of tropical species has increasingly met this demand. To reduce the impact of exploitation, many regions have put in place legislation to manage eel populations, such as the Eel Regulation (Council Regulation 1100/2007/EC) established by the European Union, and the 'Joint Statement' released by Japan, Taiwan, Republic of Korea and China. However, regulations such as these are not universal, or mandatory. Trade of certain anguillid species which are threatened, such as *A. anguilla*, have been restricted, but this has resulted in black market trade, and illegal trafficking of eels is recognised as a serious wildlife crime issue. Finally, disease and parasites also pose a threat to anguillid eel species. The catadromous, migratory nature of eels means they occupy a variety of aquatic habitats and can have high parasite and disease richness that other fish species which inhabit restricted niches. *Anguillicola crassus,* which potentially impacts migration due to swim bladder damage, is one of the most prevalent parasite threats to anguillid eel species. Disease and parasites are arguably the most recent of threats to eels, and as a result the most poorly understood.

Decline in eel populations are unlikely to be due to a single factor, it is very likely that these threats work in synergy. The impact of threats varies considerably with life stage and across the species range. As such, management measures that recognise various threats are more likely to be effective.

How can we improve the situation for anguillid eels?

Gaps in several research topics still remain for anguillid eels including life cycle and biology; threats; and management. Although a large amount of scientific literature has been produced on some anguillid eel species (e.g., *A. anguilla*), others, primarily in tropical areas, have been little-studied and major questions remain unresolved across all species, making them a rewarding and fascinating area for research. Most life history aspects of anguillid eels remain elusive or controversial and key events like spawning behaviour have only been observed in the laboratory. It is not fully known how larval eels migrate from spawning areas to the continental growth habitat, how adult eels migrate across the ocean to spawn, and which factors influence glass eel recruitment and adult eel reproductive success. How eel diet and foraging varies temporally and geographically is poorly understood, as is the proportion of eels that reside in saline waters.

In addition to a paucity of knowledge on life history, little is known about how the aforementioned threats impact anguillid eels. The full impacts of climate change, unsustainable exploitation, dam and hydropower facilities, pollution and parasites on eel stocks are unknown. Also, many questions remain on how best to manage anguillid eel stocks, the effectiveness of current techniques, the positive and negative effects of stocking anguillid eels, and how we can develop effective management frameworks to work at local, national and international levels.

In summary, anguillid eels are an incredibly mysterious and intriguing group of species. They have complex life histories, which combined with their wide geographic distribution, physiological and behaviour plasticity, and the number of potential threats they face, present a formidable challenge for their conservation and management. Rapid advancement, particularly in the last decade, in key areas including genetics, animal tracking technologies, and artificial reproduction and culture, offer great potential to unlock the outstanding mysteries and hopefully reverse the current trend of decline for anguillid eels.

Further reading

Aoyama, J. (2009). Life history and evolution of migration in catadromous eels (genus *Anguilla*). Aqua-Biosci. Monogr. 2, 1–42. https://doi.org/10.5047/absm.2009.00201.0001.

Arai, T. (2020). Ecology and evolution of migration in the freshwater eels of the genus *Anguilla* Schrank, 1798. Heliyon, 6, e05176. https://doi.org/10.1016/j.heliyon.2020.e05176

Drouineau, H., Durif, C., Castonguay, M., Mateo, M., Rochard, E., Verreault, G., Yokouchi, K., & Lambert, P. (2018). Freshwater eels: A symbol of the effects of global change. Fish Fish. 19, 903-930. https://doi.org/10.1111/faf.12300

Hsu, H., Lin, Y., Huang, Y., and Han, Y. (2020). Skin coloration and habitat preference of the freshwater Anguilla eels. Int. J. Aquac. Fish Sci. 6, 096-101. https://doi.org/10.17352/2455-8400.000063.

Itakura, H., Wakiya, R., Gollock, M., & Kaifu, K. (2020). Anguillid eels as a surrogate species for conservation of freshwater biodiversity in Japan. Sci. Rep. 10, 8790. https://doi.org/10.1038/s41598-020-65883-4

Jacoby, D.M.P., Casselman, J.M., Crook, V., DeLucia, M.-B., Ahn, H., Kaifu, K., Kurwie, T., Sasal, P., Silfvergrip, A.M.C., Smith, K.G., et al. (2015). Synergistic patterns of threat and the challenges facing global anguillid eel conservation. Glob. Ecol. Conserv. 4, 321-333. https://doi.org/10.1016/j.gecco.2015.07.009.

Jellyman, D.J. (2022). An enigma: how can freshwater eels (*Anguilla* spp.) be such a successful genus yet be universally threatened? Rev. Fish. Biol. Fish 32, 701-718. https://doi.org/10.1007/s11160-021-09658-8.

Kuroki, M., Righton, D. and Walker, A.M. (2014), The importance of Anguillids: a cultural and historical perspective introducing papers from the World Fisheries Congress. Ecol. Freshw. Fish, 23: 2-6. https://doi.org/10.1111/eff.12089.

Pike, C., Crook, V., and Gollock, M. (2020). *Anguilla anguilla*. The IUCN Red List of Threatened Species 2020: e.T60344A152845178. https://dx.doi.org/10.2305/iucn.uk.2020-2.rlts.t60344a152845178.en.

Righton, D., Piper, A., Aarestrup, K., Amilhat, E., Belpaire, C., Casselman, J., Castonguay, M., Díaz, E., Dörner, H., Faliex, E., et al. (2021). Important questions to progress science and sustainable management of anguillid eels. Fish Fish. 22, 762-788. https://doi.org/10.1111/faf.12549.

Tesch, F.W. (2003). The eel, 5th Edition (Blackwell Publishing).

Tsukamoto, K. (2009). Oceanic migration and spawning of anguillid eels. J. Fish Biol. 74, 1833-1852. https://doi.org/10.1111/j.1095-8649.2009.02242.x.

Wright, R.M., Piper, A.T., Aarestrup, K., Azevedo, J.M.N., Cowan, G., Don, A., Gollock, M., Rodriguez Ramallo, S., Velterop, R., Walker, A., et al. (2022). First direct evidence of adult European eels migrating to their breeding place in the Sargasso Sea. Sci. Rep. 12, 15362. https://doi.org/10.1038/s41598-022-19248-8.