

Anguillid eels

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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

70 al., (2021). Maximum length (L_{max} cm), where known, is given and taken from Righton et al., (2021).
 71 Dorsal colouration is taken from Hsu et al., (2020).

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

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

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.

80 *Anguillid eels – a unique life history*

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

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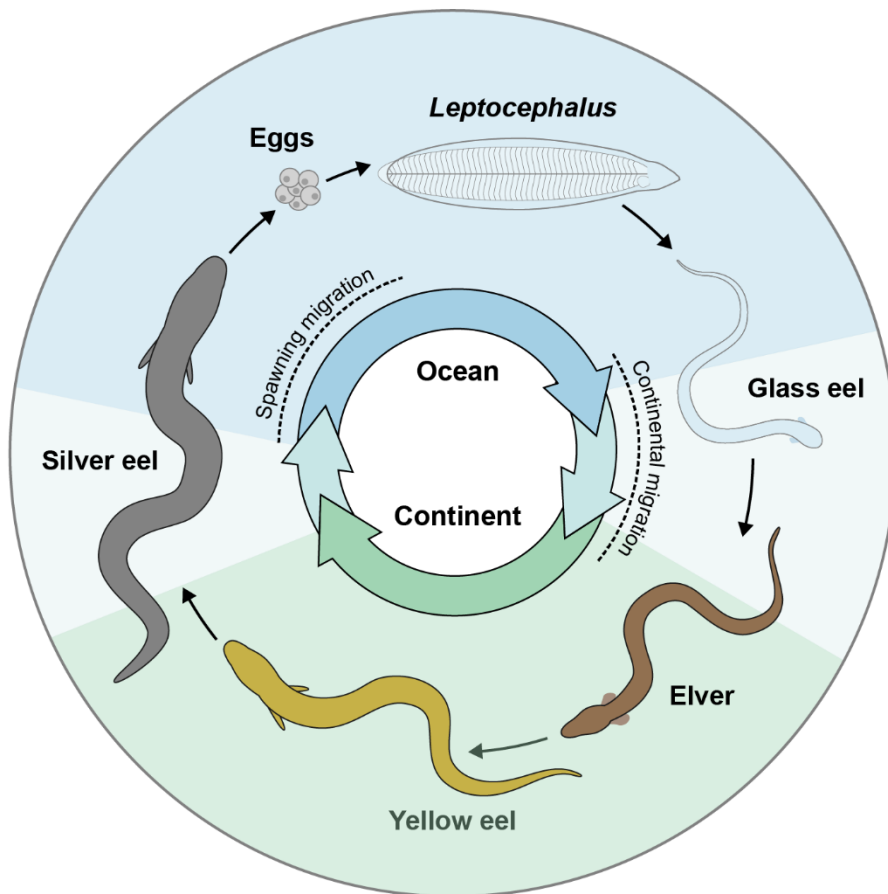


Figure 2 The catadromous life cycle of an anguillid eel.

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



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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)).

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

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128 *Anguillid eels - additional biology and ecology*

129 Anguillid eels are characterised by a slender, elongated body, notable pectoral fins, and
130 emphasised caudal fin, with other fins absent, reduced or fused with the caudal fin. Anguillid
131 eels can be separated according to morphological features e.g., bi-coloured/mottled dorsal
132 colouration or short/long dorsal fin but also in relation to their geographies e.g.,
133 tropical/temperate or Northern/Southern hemisphere (Table 1). In most species, male eels
134 grow faster than the females, and the latter generally achieve a greater age and size at sexual
135 maturity. Eel growth rate increases with temperature and is generally faster in saline water
136 than fresh. There are ontogenetic differences in preferred habitats with small individuals
137 preferring areas of shallow water and fine substrates but with increasing size eels prefer
138 greater depth. As well as these ontogenetic differences, habitat preferences may also vary
139 between species and populations. Anguillid eels are found in a range of habitats from small
140 streams to large rivers and lakes, and in estuaries, lagoons and coastal waters and are closely
141 associated with the availability of daytime cover, which can include tree roots, macrophytes
142 and anthropogenic material such as pipes and debris. During migrations anguillid eels are

143 found in open ocean habitat. However, they are rarely seen in this environment, and how they
144 utilise open ocean habitats is not fully understood.

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146 Ecologically, eels are important opportunistic predators and scavengers. Anguillid eels are
147 omnivorous, with crepuscular and nocturnal foraging patterns, and, as with habitat, diet is
148 linked with body size, as well as ontogenetic preferences. Smaller individuals feed on
149 bivalves, amphipods, shrimp and polychaete worms, with larger eels consuming larger prey
150 such as fish and crustaceans. They may even forage widely on terrestrial prey like insects and
151 earthworms during periods of increased water levels which allow them to enter newly
152 submerged areas. Eels are typically ambush predators and have different feeding mechanisms
153 ranging from suction feeding to grasping and tearing using rotational spinning. Their acute
154 olfactory sensitivity enables them to locate prey with precision. Typically, eels do not feed
155 every day, and can go long periods without feeding. For instance, *A. anguilla* have been
156 tracked undertaking their spawning migration, a non-feeding stage of their life cycle, for over
157 18 months and unfed eels kept in captivity have survived for up to five years. Anguillid eels
158 are also important prey species in the diet of a range of predators including larger eels,
159 sharks, birds, and aquatic mammals, such as otters and seals.

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161 Anguillid eels are robust, hardy and resilient fishes, and frequently survive in conditions that
162 other species cannot tolerate. They often inhabit areas with poor water quality, survive
163 droughts and, as mentioned above, can survive extended periods of fasting. Even temperate
164 species display remarkable tolerance to varying temperatures. *A. rostrata* can survive under
165 ice-covered water, below the freezing point of fish tissue, by using mud substrate as a thermal
166 refuge. Some species may also burrow into moist mud during loss of surface water enabling

167 them to survive drought conditions. Eel haemoglobin has a high affinity for oxygen and eels
168 can undergo periodic apnoea, meaning they can tolerate oxygen-depleted waters, where other
169 species cannot. Eels also have an exceptional tolerance to elevated CO₂ levels in the blood,
170 conditions associated from warm temperatures and/or eutrophication. Eels employ a buccal
171 pump system whereby the opercular chamber allows eels to respire while being immobile and
172 so they can remain motionless for extended periods. Further, they can augment gill
173 respiration with cutaneous respiration, enabling them to breathe air at the surface. The
174 widespread distribution of anguillid eels is most likely a result of their adaptability and
175 physical and behavioural plasticity, enabling them to utilise a wide range of environments
176 and habitats.

178 *Migration and movement*

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

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

201

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

207

208 *Threats to anguillid eels*

209 As anguillid eels inhabit a wide range of habitats and ecosystems they can serve as indicator,
210 umbrella and flagship species for conservation of aquatic biodiversity. However, many
211 anguillid eel species have undergone a dramatic decline in only a few decades. Of the
212 recognised 19 species and sub-species, six are listed in Threatened categories (Vulnerable,
213 Endangered, Critically Endangered) on the IUCN Red List of Threatened Species. This could
214 be greater with four of the tropical species listed as Data Deficient, where there is not enough

215 information to be assigned a category. The three most economically important species are
216 listed as either Critically Endangered (*A. anguilla*) or Endangered (*A. rostrata*, *A. japonica*).
217 These declines have been driven by a number of threats, such as climate change; pollution;
218 barriers to migration; unsustainable exploitation; and disease and parasites.

219

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

231

232 Fragmentation resulting from the construction of riverine barriers (e.g., weirs and dams) have
233 particularly detrimental impacts on eels. This is mainly through reducing access to growth
234 habitat, altering distributions, restricting migrations, increasing energy costs, as well as direct
235 mortality and sublethal injuries through encountering turbines and water pumps or
236 impingement on hard structures such as screens. To increase connectivity and reduce impact
237 of barriers, mechanisms have been added to exclude eels from harmful areas, such as intakes,
238 and guide them to safe downstream passage routes using physical (e.g., screens, guiding

239 walls and passes/fish lifts) or behavioural (e.g., hydraulic, light, acoustic) measures.

240 Unfortunately, there is no single technique that can be universally applied, and efficiency of
241 applied systems remains low.

242

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

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261 Decline in eel populations are unlikely to be due to a single factor, it is very likely that these
262 threats work in synergy. The impact of threats varies considerably with life stage and across

263 the species range. As such, management measures that recognise various threats are more
264 likely to be effective.

265

266 *How can we improve the situation for anguillid eels?*

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

278

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

286

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.

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