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POINT-OF-VIEW

# An enigma: how can freshwater eels (*Anguilla* spp.) be such a successful genus yet be universally threatened?

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**Abstract** Freshwater eels are of tropical marine origin and have spread worldwide. Of the 19 recognised species or subspecies, all 6 temperate species are listed within IUCN Threatened Species categories, together with 7 tropical species. Many reasons have been advanced to explain the significant declines of eels including habitat fragmentation and loss, spread of parasites and diseases, pollution, impacts of hydro dams, overfishing and oceanic changes. The present paper reviews some of the unique life history characteristics of Anguillids—fecundity and semelparous spawning, adaptability, resilience, and being energetically conservative—but despite such remarkable adaptations, according to the IUCN the genus is facing possible extinction. It is suggested that Anguillid life history strategies rely on two additional components—environmental determination of sex, and the need for surplus production (the Surplus Production Hypothesis, SPH). Surplus production is required to counteract the many hazards that eels face throughout an often long and complex life history. Recruitment of temperate species has fallen by over 90%, and resulting lower densities of juvenile eels in tidal and lower river reaches provides less incentive for upstream migration and dispersal. Female eels are generally found further inland than males, with development of sex associated with lower densities. With fewer juveniles migrating to inland areas, the numbers of females will become reduced, and further compound the reduced spawner biomass and consequent reduced recruitment of glass eels. The SPH hypothesis emphasises the importance of conservative harvest of glass eels, habitat connectivity, the need to ensure maximum female escapement, and the importance of stocking inland waterways with juvenile eels.

**Keywords** Anguillids · Threatened species · Surplus production · Recruitment · Fecundity · Resilience

## Introduction

Freshwater eels (Anguillidae) are a highly successful group of diadromous fish. The genus comprises 19 recognised species or sub-species (Kaifu et al. 2019), of which 13 are tropical and 6 are temperate. The marbled eel, *A. marmorata* has the greatest geographic range of any anguillid species, being found from the east coast of Africa to the Galapagos islands (McCosker et al. 2003), while *A. anguilla* occupies over 10,000 km$^2$ (Dekker 2008). The American eel, (*Anguilla rostrata*) is found along more than 10,000 km of the western Atlantic coastline, leading to the claim by Helfman et al. (1987) that it probably occupies the broadest diversity of habitats of any fish

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species in the world. As well as being widespread, eels have colonized an extensive range of inshore marine and freshwater habitats worldwide, including estuaries and coastal embayments, mainstem rivers, swamps and wetlands, lowland and inland lakes, ranging from oligotrophic to eutrophic (Dekker 2008). Thus, anguillids will have the widest distribution of any naturally occurring freshwater genus.

## Origins and Life history

The genus originated in tropical marine areas but has since colonised freshwater habitats (Tseng 2016; Arai 2020). Thirteen species live in the Indo-Pacific region (Tseng 2016), considered to be the ancestral home of the genus (Minegishi et al. 2005). The ancestor of *Anguilla* probably originated in the Tethys Sea 50–100 Mya, but closure of this sea separated the Atlantic eels from Indo-Pacific eels, leading to the vicariant speciation of other Anguillid species (Tseng 2016). With the exception of the New Zealand longfin (*A. dieffenbachii*), all anguillids today range at least partially in tropical and subtropical areas (Nijman and Siriwat 2020).

Being of marine origin, the genus retains marine spawning, with dispersal of larvae (leptocephali) being largely passive on favourable ocean currents that convey larvae to island and continental waters. For temperate species, distances from spawning areas to freshwater habitats are measured in 1000’s of km—the greatest distance traversed is by *A. anguilla*, the European eel, where migrations range from 5000–10,000 km (Righton et al. 2016). In contrast, the spawning ground for *A. celebesensis,* a tropical species, is probably less than 100 km from adult habitat (Aoyama et al. 2003; Arai 2016). However, the scale of spawning migrations of tropical species varies considerably with some species undertaking migrations between 1000–3000 km (Arai 2020). While dependence upon larval dispersal by oceanic currents has been an effective one for colonisation of widespread regions, it is also a constraint as lack of suitable currents means freshwater eels are absent from significant areas of the world, notably western coasts of Africa and North America, and South America.

When they arrive over continental shelves, the larvae metamorphose from the leaf-shaped leptocephalus to a miniature version of the elongate and slender adult, the transparent glass eel. This is the stage of entry to fresh water, and while a proportion of glass eels may choose to reside in estuarine and brackish water, most will continue their inland penetration the following summer as pigmented juveniles, elvers (Jellyman 1977; Naismith and Knights 1988; Jellyman and Arai 2016). While there are ontogenetic differences in preferred habitats occupied (Laffaille et al 2003; Jellyman et al 2003), eels will often inhabit the same general area for several years. While freshwater eels are catadromous, this behaviour is facultative as both yellow and silver eels of temperate and tropical species are capable of living their entire lives in coastal marine habitats (e.g. Tsukamoto and Arai 2001; Daverat et al. 2006; Jessop et al. 2008; Arai 2020). Eventually adult eels undergo a second metamorphosis and become silver eels, the stage of emigration to the spawning grounds. This is a fasting stage. It is assumed that eels die after spawning due to the huge energetic demands of both oceanic migration and spawning, and the severe weight loss and organ degeneration of post-spawned eels (Kurogi et al. 2011).

## Importance and status of species

Ecologically, eels are very important opportunistic predators and scavengers, and serve as indicator, umbrella and flagship species for conservation of freshwater biodiversity (Itakura et al. 2020). Eels can often dominate fish biomass (Rowe et al. 1999), and, at least at historic high levels of recruitment, constrained populations of other species (Burnet 1968; Dorner and Berg 2016). Eels are also important in the diet of a range of predators including larger eels (Jellyman 1989), birds (Leukona 2002) and otters (*Lutra lutra*; Jenkins and Harper 1980; Kruuk 2014). Additionally, freshwater eels are commercially important, providing an international trade of almost 270,000 t in 2014, of which 98% was cultured (Monticini 2014). Unlike most commercially important fish species that are usually harvested as adults, eels are exploited at all continental life stages i.e. glass eels, elvers, yellow eels, silver eels. The demand for glass eels for culture in Asia has led to the prohibition of export of *A. anguilla* glass eels beyond EU borders, but unfortunately a lucrative illegal market has developed, trafficking an estimated 100 t ($\sim$ 350 million fish) annually (Kaifu et al. 2019). Eels are of great importance to native peoples, both as a foodstuff but also as a species of cultural significance (Tsukamoto and Kuroki 2014)—for example, there are many legends of the interactions of eels and human ancestry in the South Pacific (e.g. Downes 1918; Jellyman 2014).

Historically, eels were much more prolific than at present. In medieval England they were once so plentiful that they were used as currency (https://www.historyextra.com/period/medieval/eels-medieval-life-eel-rent-economy). Ribbons of glass eels migrating upstream could be seen in many European rivers (Tesch 2003), and have been described in the United Kingdom as "dense ribbons of fish, hundreds deep and tens of miles long" (Righton and Roberts 2014) and providing a black margin to either bank of the River Thames (Cornish 1902). A shoal in the Waikato River, New Zealand (4.5 m wide and 2.5 m deep) took over 8 h to pass a stationary point (Cairns 1941), while reports of continuous migrations lasting several days were not uncommon (Jellyman 1979). Glass eels were so abundant and widely available they were an important traditional food source in many European countries (Hunt 2007; McCarthy 2014). Numbers are staggering—for instance, the peak European glass eel catch in 1976 of 2700 t would equate to approximately 6.7 billion glass eels (Jellyman and Briand 2016). However, since 1980, recruitment of *A. anguilla* glass eels has fallen to 1–10% of former levels and in recent decades the yield of *A. anguilla* from eel fisheries has gradually declined to $\sim$10% of the quantity caught just half a century ago (Dekker and Beulaton 2016).

Overall, the genus is in a parlous state. Of the recognised 19 species and sub-species, 4 of the tropical species are listed by IUCN (2017) as Data Deficient so cannot be assessed but 7 of the remaining 9 tropical species are within Threatened Species categories (Near Threatened, Vulnerable, Endangered, Critically Endangered), while all 6 temperate species are within this Threatened Species classification (Table 1). The three species most important to world economy, are either critically endangered (*A. anguilla*) or endangered (*A. rostrata, A. japonica*).

There is a huge assemblage of scientific studies on Anguillid eels. For instance, Table 2 shows the genus *Anguilla* has 179,000 references in Google Scholar (Table 2), and while that is exceeded by other "freshwater" species, it exceeds references for common marine genera. Despite such scientific endeavour, many of the life history aspects of *Anguilla* remain elusive or controversial and key events like spawning behaviour have only been observed in the laboratory (Dou et al. 2007). Age and growth studies dominate the literature from the 1970's to 2010 for the European eel (14%), followed by aquaculture (13%), diseases (10%), migration (10%), abundance (10%), and fisheries (8%), but studies on the impacts of climate change and resource management were low but increasing (Nikolic et al 2011).

## Purpose of this paper

Much has been written about possible causes of the alarming decline of northern hemisphere eels (e.g. Dekker 2003, 2008; Haro et al. 2000; Feunteun 2002; Miller et al. 2009; Kettle et al. 2011; ICES 2014; Jacoby et al. 2015; Castonguay and Durif 2016; Drouineau et al. 2018). Possible reasons include reduction and loss of freshwater habitats, spread of parasites and diseases, pollution, impacts of hydro dams, overfishing of all freshwater stages, and oceanic changes, but most authors concede that it is very likely a combination of factors are involved (e.g. Dekker 2009). Drouineau et al. (2018) suggest that although eels are highly adaptable, the rate of anthropogenic change has exceeded their adaptive capacity, with resultant drastic declines in northern hemisphere species. Most reviews have concentrated on the potential impacts of physical changes to the eel's environment and have been less focused on how unique *Anguilla* life history strategies might be involved. The present paper examines aspects of eel life history to explore why such an apparently successful genus is now almost universally threatened. Firstly, the paper highlights some of the unique adaptations of freshwater eels that have led to their widespread distribution and success in colonising an extensive range of habitats. Secondly, the paper discusses why such strategies that have been successful over geological time scales, appear less successful in the Anthropocene era.

**Table 1** Status of *Anguilla* species (from IUCN 2017)

| Type | Species | Common name | Distribution | Status |
|---|---|---|---|---|
| Tropical species | *A. luzonensis* | Philippine mottled eel | Northern Philippines | VU |
| | *A. interioris* | Highland longfin | Endemic to northern half of New Guinea | DD |
| | *A. bengalensis bengalensis* | Indian mottled eel | South Asia and southeast Asia | NT |
| | *A. bengalensis labiata* | Indian mottled eel | East coast of Africa (Kenya to South Africa) | NT |
| | *A. obscura* | Pacific shortfin | Western New Guinea, Solomon Islands, Fiji, French Polynesia | DD |
| | *A. bicolor bicolor* | Shortfin | East Africa, Arabian Peninsula, Indian Ocean Islands, southeast Asia, | NT |
| | *A. bicolor pacifica* | Shortfin | East Asia and Southeast Asia | NT |
| | *A. marmorata* | Marbled eel | Pacific and Indian Oceans. East Africa, India, Sri Lanka to the Indo-Pacific region (East Asia, Southeast Asia, the Pacific and South Pacific islands) | LC |
| | *A. celebsensis* | Celebes longfin | Western Pacific from Indonesia to southern Philippines | DD |
| | *A. megastoma* | Pacific longfin eel | Endemic to the Western and Central Pacific islands (Pitcairn to Papua New Guinea) | DD |
| | *A. reinhardtii* | Australian longfin | East Coast of Australia, Tasmania, northern New Zealand | LC |
| | *A. borneensis* | Indonesian longfin | East Sumatra | VU |
| | *A. mossambica* | African longfin | South West Indian Ocean (African east coast and Indian Ocean islands) | NT |
| Temperate species | *A. anguilla* | European eel | United Kingdom, Europe, north Africa | CR |
| | *A. rostrata* | American eel | East coast of United States and Canada | EN |
| | *A. japonica* | Japanese eel | Japan, Korea, Taiwan, China, northern Philippines | EN |
| | *A. australis australis* | Australian shortfin | East Coast of Australia, Tasmania, New Caledonia | NT |
| | *A. australis schmidtii* | New Zealand shortfin | New Zealand, Fiji | NT |
| | *A. dieffenbachii* | New Zealand longfin | New Zealand | EN |

DD = data deficient, LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered

## Life history features that make major contributions to the success of Anguillid eels

Eels are amazing creatures and endowed with a unique set of morphological and behavioural features that collectively have enabled them to become such a successful and widespread genus. Five of these features are foundational to this success i.e. semelparous spawning, high fecundity, adaptability, resilience, and being energetic conservative (note that because semelparous spawning and fecundity are

**Table 2** The number of references for selected freshwater and marine genera retrieved by Google Scholar (as at April 2021, June 2020)

| Species habitat | Genus | Number of references |
|---|---|---|
| Freshwater | *Salmo* | 510 000 |
| | *Tilapia* | 438 000 |
| | *Cyprinus* | 298 000 |
| | *Anguilla* | 179 000 |
| | *Perca* | 179 000 |
| Marine | *Gadus* | 136 000 |
| | *Thunnus* | 71 300 |
| | *Clupea* | 66 100 |

highly inter-related, they are combined in the following discussion).

## Semelparous spawning and fecundity

Freshwater eels, like Pacific salmon, are semelparous species, and invest heavily in a single reproductive effort, after which the parents die. Much has been written about the evolution and relative advantages of semelparity versus iteroparity (e.g. Cole 1954), and for eels it is characterised by the production of numerous small eggs rather than fewer larger eggs, presumably as success of pelagic spawning is more strongly associated with egg numbers than egg size (Duarte and Alcaraz 1989). While iteroparity might be sustainable for tropical eels with shorter marine migrations, it would not be suitable for temperate species that undergo extensive migrations unless it were accompanied by feeding *en route;* however, given that eels are principally benthic ambush carnivores, this would not be a successful strategy in the open ocean.

Many fish species use a form of "bet-hedging" (e.g. partial spawning, parental care) to provide some buffer against such adverse effects as high predation or significant environmental change. Being complete spawners, eels do not exhibit bet-hedging at spawning; however, as sexual maturity is not dependent upon achieving a specific size or age, the spawning population will be comprised of many age cohorts—for example, ages of silver *A. dieffenbachii* females can range between 25 and 60 years (Todd 1980). Such a mixed age cohort spawning strategy reduces the risk of overall spawning failure by diluting the impacts of both poorly and well represented cohorts.

Semelparity is an "all eggs in one basket" strategy, as eels risk spawning failure due to such factors as insufficient energy reserves to swim to the spawning grounds (van den Thillart et al. 2009), high loadings of the swim bladder parasite, *Anguillicola,* that can impair swimming performance (Székely et al. 2009), predation *en route* (Béguer-Pon et al. 2012; Wahlberg et al. 2014), failure to navigate to the spawning ground, and failure to find a mate. In addition, the conveying of larvae back to parental habitats requires stability in the strength and direction of ocean currents. To compensate for such uncertainties and risks, eels, like other broadcast spawning fish (e.g., tuna, Farley et al. 2013) are highly fecund. Fecundity in eels is positively related to fish size (Todd 1981; MacNamara and McCarthy 2012), and females adopt a size-maximising strategy (Helfman et al. 1987). Actual fecundity varies with species and size, but recorded values range between 0.3–192.9 m eggs per female (Table 3).

## Adaptability

Anguillids display remarkable adaptability during their freshwater residence. Most will enter fresh water, but many have extended or permanent residence in marine or estuarine environments (Tsukamoto and Arai 2001). The habitats they occupy change with growth—small individuals often prefer areas of shallow water and fine substrates (Jellyman et al. 2003; Johnson and Nack 2013), but with increasing size, eels prefer greater depth. At all freshwater stages, eels are closely associated with the availability of daytime cover, which can range from riparian shade and tree roots, debris clusters, undercut banks, macrophytes, and anthropogenic material like bridge piles, pipes and other debris. The climbing ability of juvenile eels (Skead 1959; Jellyman 1977) allows them to negotiate waterfalls, dams and weirs, and they can also travel through subterranean aquifers and enter coral atolls via subsurface outfalls (Castle 1968; Jellyman 1991).

Despite being primarily nocturnally active (Tesch 2003; Glova and Jellyman 2000), eels will actively feed during the day if food is available. Their diet changes with size (Jellyman 1989; Tesch 2003; Dörner and Berg 2016), and while they display ontogenetic feeding preferences (e.g. Sagar et al. 2005; Jellyman

**Table 3** Summary of anguillid fecundity studies. (Note that a more complete compilation of fecundity data for *A. rostrata* is contained in Jessop 2018)

| Species | References | Length range (mm) | Number of eels examined | Min–max fecundity (millions of eggs) | Relative fecundity (millions of eggs/kg) |
|---|---|---|---|---|---|
| *A. anguilla* | Boetius and Boetius (1980) | 519–1339 | 29 | 0.7–2.6 | 1.6 |
| | van Ginneken et al. (2005a) | 690–870 | 7 | 0.8–4.0 | |
| | MacNamara and McCarthy (2012) | 465–1003 | 38 | 0.6–8.0 | 3.6 |
| | MacNamara et al. (2016) | 465–1003 | 170 | | 3.6–4.3 |
| *A. rostrata* | Wenner and Musick (1974) | 490–724 | 41 | 0.5–2.6 | 3.8 |
| | Barbin and McCleave (1997) | 452–1133 | 64 | 1.7–20.7 | 8.1 |
| | Verrault (2002) | 743–1117 | 30 | 2.9–14.1 | 2.0–4.4* |
| | Tremblay (2009) | 532–1159 | 150 | 2.9–22.0 | 6.5–10.0 |
| *A. australis* | Todd (1981) | 516–933 | 26 | 0.5–3.0 | 1.9 |
| *A. dieffenbachii* | Todd (1981) | 711–1452 | 23 | 1.1–20.8 | 2.0 |
| *A. japonica* | Matsui (1952) | 357–924 | | 7.2–12.7 | |
| *A. marmorata* | Sugeha et al. (2001) | 940–1725 | 9 | 34.8–192.9 | 14.3 |
| | Abdul Kadir et al. (2017) | 904 | 9 | 1.0 | 0.42 |
| *A. bengalensis bengalensis* | Abdul Kadir et al. (2017) | 899–1295 | 7 | 0.3–1.7 | 0.34 |
| *A. bicolor bicolor* | Abdul Kadir et al. (2017) | 567–810 | 15 | 0.6–5.0 | 3.1 |

* = estimated from mean size and fecundity data

1989), they are opportunist scavengers and eat a wide range of prey species. This opportunist behaviour is perhaps best demonstrated during periods of increased flow, when eels will enter newly inundated areas and forage widely on terrestrial food like insects and earthworms (Jellyman 1989). Although their maintenance ration is $<1\%$ of body weight (Burnet 1952; Graynoth and Taylor 2000), their stomach is extensible, and they can consume $\sim 10\%$ of body weight/day (Gousset 1992).

Eels have different feeding mechanisms ranging from suctorial feeding via rapid buccal suction to grasping and tearing using rotational spinning (Helfman and Clark 1986). Typically, eels do not feed every day (Jellyman 1989), and can survive extended periods of fasting—for instance, the silver eel migration of several months is a non-feeding stage, and eels kept in captivity and not fed have survived for up to 5 years (Olivereau and Olivereau 1997). Growth rates are highly variable, ranging from achieving 200 g in 6 months in culture (Gousset 1992), to growing at $<1$ cm/year and reaching $>100$ years old (Jellyman 1995).

The determination of sex in eels is labile, and predominantly a response to growth rates and population density (Davey and Jellyman 2005), 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 inland (Tesch 2003; Oliveira and McCleave 2000; Walsh et al. 2004).

Phenotypic plasticity in eels is demonstrated by their use of diverse growth habitats (Daverat et al. 2006; Edeline 2007), variable growth rates (Geffroy and Bardonnet 2012) and length at silvering (Vollestad 1992). The seaward migration of silver eels can be delayed for a year or more should environmental conditions be unfavourable (Piper et al 2013; Jellyman and Unwin 2017). Collectively, such physical and behavioural plasticity results in considerable risk spreading and is suggested as one of the main reasons contributing to eel's widespread distribution and colonisation of a wide range of marine and freshwater habitats. In colloquial terms, eels "go with the flow", and their adaptive abilities enable them to utilise a wider range of environments and habitats that any other freshwater genus.

## Resilience

Eels are hardy. They can tolerate water quality conditions that few other species can and survive droughts and extended periods of fasting. Tropical species are adapted to warm temperatures, hence the conclusion of Luo et al. (2013) that *A. marmorata* and *A. bicolor pacifica* survive and grow better at water temperature of 28–33 °C than at temperatures of $\leq$ 23 °C. However, even temperate species display remarkable tolerance of warm water, and Richardson et al. (1994) found the upper lethal temperatures for *A. australis* were 35.7 °C for juveniles and 39.7 °C for adults, with equivalent data for *A. dieffenbachii* being 34.8 °C and 37.3 °C respectively, similar to the upper limit of 38 °C for *A. anguilla* (Sadler 1979).

They also survive low temperatures, and between 1 –3 °C, *A. anguilla* enter a state of torpor (Sadler 1979). While *A. rostrata* survived at $\leq$ 5 °C for more than five weeks, the fish ceased feeding and displayed a dramatic decrease in oxygen consumption rates (Walsh et al. 1983). *A. rostrata* can survive under ice-covered water, where the temperature is below the freezing point of fish tissue, probably by using mud substrate as a thermal refuge (Tomie et al. 2016). Silver eels are known to use low temperatures during winter to enter a state of dormancy prior to emigration (Westerberg and Sjoberg 2014; Jellyman and Unwin 2019).

Eels subject to drought conditions do not aestivate but are able to lower their metabolic demands by up to 70% during periods of anoxia (van Ginneken et al. 2001), a practice that will enhance survival during such adverse conditions. In New Zealand, *A. australis* often survive loss of surface water by burrowing into moist mud (Eldon 1968; https://www.stuff.co.nz/the-press/news/north-canterbury/89068402/mata-kopae-lagoon-vanishes).

Eels can survive in oxygen-depleted waters (Wood and Johansen 1973) where more active species cannot. This survival in hypoxic conditions is due to such features as their blood having a high affinity for oxygen, and periodic apnoea (Forster 1981). Eels also have an exceptional tolerance to elevated $CO_2$ levels in the blood (hypercapnia; McKenzie et al. 2002), conditions associated with hypoxic conditions resulting from warm temperatures and/or eutrophication. Further, they can augment gill respiration with cutaneous respiration (Forster 1981), and when dissolved oxygen levels fall below 10%, they will frequently come to the water surface and gulp air, or leave the water altogether (Itazawa 1960). The tenacity for life shown by eels is legendary, and they can even survive severing of the nerve cord (Flight and Verheijen 1993), so that humane killing requires destruction of the brain itself. Under adverse environmental conditions like low flows, eels tolerate living in close proximity. Crowding reaches extremes in culture where eels can be reared in high densities (e.g. 15 kg/m$^3$ Gousset 1992); agonistic interactions do occur but can be reduced by size grading (Knights 1987).

So, Anguillids are hardy and resilient fishes, and frequently survive in conditions that other species cannot tolerate. This resilience is apparent at all life stages, but particularly during the yellow eel stage in coastal or freshwaters where physiological robustness aided by the eel's sinuous shape, enables penetration of aquifers, and even climbing near-vertical surfaces. Eels rapidly colonise newly available habitats (Briand et al. 2005) or even temporary habitats like water storage ponds (author. unpubl. data), and in many ways exemplify the colloquialism "when the going gets tough, the tough get going".

## Energetically conservative

Many of the features listed in the above sections on adaptability and resilience result in reduced energy expenditure by eels—for example, being relatively inactive during daylight, and able to feed sporadically and endure prolonged fasts. Their acute olfactory sensitivity enables them to locate prey with precision, thus avoiding extensive searching behaviour; for larger individuals, adoption of piscivory means utilising larger prey species with high energy content, often captured from ambush using macrophyte beds for concealment (Burnet 1952), again reducing energy expenditure. Their use of cover and crevices for concealment avoids the need to maintain station in flowing water conditions, and this is even more evident in juvenile eels that spend most of their time within substrates (Burnet 1952; Glova and Jellyman 2000).

Eels employ a buccal pump system whereby the opercular chamber functions as a pump, enabling eels to respire while being immobile. Thus they can remain motionless for extended periods, whether diel (Baras et al. 1998; Jellyman and Sykes 2003) or seasonal (Westerberg and Sjoberg 2014). Their sinuous swimming action is energetically conservative and efficient for long distance travel (van Ginneken et al. 2005b). In swimming tube trials to study the effect of continuous swimming for 5500 km (equivalent to swimming from Europe to the Sargasso Sea), van Ginneken et al. (2005b) found that eels could accomplish this with expenditure of only 40% of their stored fat reserve (van Ginneken and van den Thillart 2000), and their swimming action was 4–6 times more efficient than non-eel-like fish. To use a human metaphor, eels are built for a marathon not a sprint.

Eels take advantage of passive transport from oceanic, tidal and river currents. Thus, leptocephali are largely carried along by favourable ocean currents, while glass eels use selective tidal transport to enter rivers and migrate upstream (Creutzberg 1961; Jellyman 1979). Silver eels usually emigrate downstream during periods of increased flow (e.g. Bruijs and Durif 2009) and mainly use the centre of main river channels to ensure they derive maximum benefit from currents (Euston et al. 1998; Jansen et al. 2007; Behrmann-Godel and Eckmann 2003) and avoid bankside obstacles. Even at sea, silver eels are known to use selective tidal stream transport (McCleave and Arnold 1999), and it is speculated that they may use directional tidal streams to cross the continental shelf (van Ginneken and Maes 2005).

Overall then, eels largely sedentary mode of life in freshwater, combined with an efficient swimming action and their widespread use of currents, means they are energetically conservative species, yet able to draw upon considerable reserves of stored energy when required for long distance migration. In many ways they epitomise Aesop's fable of the hare and tortoise that "slow and steady wins the race".

## Exploring the enigma

So, anguillids are a very successful genus, inhabiting many countries and a wide range of habitats, largely due to their extraordinary life history features of semelparous spawning and high fecundity, adaptability, resilience, and being energetically conservative. Given such physical and physiological versatility, it seems incongruous that the genus is in a parlous state worldwide. What has changed over the past few decades that has led to such a dramatic decline in the fortunes of these highly successful species?

The drastic reductions seen in stocks of many eel species may be largely a consequence of the reduced effectiveness of two fundamental life-history drivers, i.e. environmental determination of sex (EDS), and the need for surplus production (the Surplus Production Hypothesis, SPH). While the former process has been long known and extensively discussed (e.g. Beullens et al. 1997; Krueger and Oliveira 1999; Davey and Jellyman 2005; Melia et al. 2006), SPH is a new hypothesis and suggests that the risks associated with semelparous marine spawning are offset by surplus production of juveniles—a type of insurance against adversity.

In general, EDS is an advantageous mechanism and can ameliorate the effects of reduced stock levels. Limiting factors for successful spawning and subsequent recruitment to landmasses will be more associated with abundance of spawning females than males—theoretically, a few males could inseminate the total female spawner biomass (although in practice, spawning behaviour and disparate spawning locations will inevitably require the presence of many males). There is little reproductive advantage to males in achieving large size, and their strategy is one of growing as rapidly as possible to a size where they have the ability and enough stored energy to sustain a long-distance spawning migration (Helfman et al. 1987; Vollestad 1992). As eel stocks diminish, reduced densities will favour production of females, a feature of EDS that should provide some buffer against overall reduced numbers of fish. Thus, with reduced recruitment, populations have been found to change from male-dominated to female-dominated (Laffaille et al. 2006; Bark et al. 2007).

## Surplus Production in *Anguilla* life history

Surplus production is suggested as an essential and allied component to EDS in eel life histories. Further, success of the *Anguilla* life history strategy is dependent upon a surplus in overall recruitment, and recruitment failure in turn has led to negative cascades in eel population size and reduced numbers of female silver eels.

SPH is demonstrable at spawning and recruitment of anguillids. High fecundity and mass spawning events should result in vast numbers of larvae. Essentially, semelparous spawning at distant locations is a "numbers game", such that large number of offspring are required to ensure successful recruitment. Spawning over widespread areas (a 2000 km wide region for *A. anguilla*, Miller et al. 2019) could provide some buffer against localised spawning failure or development of unfavourable currents to transport larvae. Little is known about the behaviour and mortality of leptocephali—they can be found over vast areas (Miller et al. 2019) and their transparency presumably reduces the likelihood of predation (Miller 2009). Although they are capable swimmers and undergo diel vertical migrations (Miller 2009), there is no evidence that they form shoals, a feature that should enhance survival as shoals attract predators whereas it can be less energetically efficient for predators to pursue individual fish.

To arrive at continental destinations, leptocephali must become entrained in favourable currents. This process can be problematic. For instance, for *A. japonica,* the North Equatorial Current is the main vector transporting larvae westwards, but whether larvae then get transported north in the Kuroshio Current or south in the Mindanao Current depends on where the larvae are located in relation to the current bifurcation and the location of the salinity front (e.g. Kim et al. 2007). For *A. rostrata*, arrival at continental North America requires detrainment from the Gulf Stream, and failure to do so would result in continued transport towards Europe. Recent drift model simulations of larval *A. anguilla* and *A. rostrata* have indicated that the majority of leptocephali may become trapped in unfavourable areas of the Sargasso Sea and die, with only a small proportion becoming entrained in the Gulf Stream (Westerberg et al. 2018).Thus, high fecundity is required to compensate for the collective risks of larval mortality.

## Importance of SPH

SPH would benefit eels in several ways:

- *Overall survival* Eels are subject to mortality at all phases of their lives, whether in the open ocean or in fresh water. To be successful, semelparity requires a sufficient number of yellow eels to survive to silvering. Historically it is suggested that SPH provided an adequate safeguard against survival uncertainty, but of particular concern at present is the overlay of anthropogenic mortality upon an already risk-prone life history.
- *Predator satiation* The synchronised shoaling behaviour of large numbers of glass eels and juvenile pigmented eels (elvers) migrating upstream will enhance their survival through predator satiation (e.g. Gill 2003). During such migrations, these juvenile eels are subject to a barrage of aquatic and avian predators (Leukona 2002; Jenkins and Harper 1980), but their sheer numbers will result in predators becoming satiated and confused (e.g. Ioannou et al. 2008) and enhance overall rates of survival.
- Mass recruitment into estuarine areas is a trigger for subsequent upstream migration and dispersal of juveniles—the arrival of large numbers of new recruits into population-saturated areas results in density-dependent upstream migrations of previously-resident juveniles (Lobon-Cervia et al. 1995; Feunteun et al. 2003; Ibbotson et al. 2002; Briand et al. 2005; Edeline et al. 2007). Agonisitc behaviour and cannibalism will also reinforce such annual upstream migrations (Edeline et al. 2009). Annual upstream migrations will persist in individuals for several years (e.g. Naismith and Knights 1988; Jellyman and Ryan 1983). It is suggested that this process is an essential outcome of SPH as it results in colonisation of upstream parts of catchments where the reduced density of eels will result in a high proportion developing as females. The urge to migrate upstream will be reinforced by the odour of conspecifics (Galbraith

et al. 2017)—reduced numbers of juvenile eels upstream would provide fewer olfactory cues and consequently fewer responses from downstream juveniles.

- Reduced recruitment results in range contraction. As glass eel recruitment declines, it is most obvious at the extremes of the natural range—thus, recruitment to the Baltic Sea (both natural and by stocking) has declined by 95% between 1981 and 2012 (Westerberg and Wickström 2016). A number of studies of *A. rostrata* and *A. anguilla* have shown that the size of female silver eels increases and the proportion of males decreases with increasing latitude and distance from spawning areas (Helfman 1988; Oliveira 1999; Jessop 2010; Vøllestad 1992). As recruitment to such areas declines, the contribution of these large, fecund eels will be lost.
- SPH ameliorates interannual variability in cohort strength. Unlike Pacific salmon (*Oncorhynchus* spp.) that spawn at pre-determined ages, female silver eels are comprised of multiple cohorts so the impact of periodic weak recruitment will not be discernible as a result of varying growth rates and ages at silvering.

A diagrammatic comparison of *Anguilla* historic (A) and present day (B) life history strategies (Fig. 1) shows the likely influence of EDS and SPH.

## Vulnerability of SPH

A strategy like SPH is particularly vulnerable at two stages—a reduction in spawner biomass and variability in oceanic conditions that convey larvae back to inshore marine and freshwater habitats. Miller et al. (2016) proposed that a "perfect storm" of simultaneous oceanic changes and continental anthropogenic impacts could have led to recruitment reductions of northern hemisphere anguillids, with both sets of factors possibly acting synergistically. Variability in oceanic fronts (Miller et al. 2016), latitudes of bifurcation of currents (Zenimoto et al. 2009), and temperature and productivity changes associated with phase shifts in NAO (North Atlantic Oscillation) and ENSO (El Nino-Southern Oscillation) have all been associated with subsequent changes in juvenile eel recruitment (e.g. Knights 2003; Friedland et al. 2007; Bonhommeau et al. 2008a, b; Kettle et al. 2008; Durif et al. 2011; Arribas et al. 2012; Miller et al. 2016). The synchronous decline of northern hemisphere species over similar time scales points to widespread changes in oceanic conditions being a primary cause (Bonhommeau et al. 2008a; Drouineau et al. 2018). It is also possible that spawning over widespread areas means eels are subject to Allee effects whereby the chances of successful mating become drastically less as the number of available spawners declines (Poole et al. 2018), possibly as a result of failure to find mates or some behavioural aspects of social mating behaviour (Dekker 2008). Of course, all such marine life history lies beyond the sphere of immediate human influence, meaning that attempts at stock restoration must focus on the continental phase.

Maximising the production of female silver eels is proposed as the single most effective management tool for conservation of the genus, but to achieve this females have to survive a barrage of threats for many years. These threats include extensive habitat loss and fragmentation (e.g. Chen et al. 2014), accumulation of toxicants (Robinet and Feunteun 2002), transfers of parasites and diseases (Castonguay et al. 1994), barriers to movements (e.g. Laffaille et al. 2005; Piper et al. 2013), targeted fishing/overfishing by commercial and artisanal fishers (e.g. Jellyman 2014, 2016).

Upstream migrations of juvenile eels are often hindered by the lack of riverine connectivity due to weirs and dams; for example Busch et al. (1998) state that more than 15,000 dams have been built in North Atlantic coast drainages, blocking direct access to ~87% of river and stream reaches flowing into the Atlantic, which has resulted in a greatly reduced inland range of the American eel (Miller and Casselman 2014). Restoration of connectivity via dam removal led Hitt et al. (2012) to conclude that restoring connectivity to headwater streams could increase eel population growth rates by increasing female eel numbers and fecundity.

Not only does reduced recruitment result in less upstream movement of juvenile eels and fewer females, but those females that do eventuate and become silver eels often have to run a gauntlet of dams, weirs, pumping station etc. before they are able to enter the sea. Again, much has been written about turbine mortality of female eels (e.g. McCleave 2001; Richkus and Dixon 2003; Verreault et al. 2004; Buysse et al. 2013; Heisey et al. 2019), and being

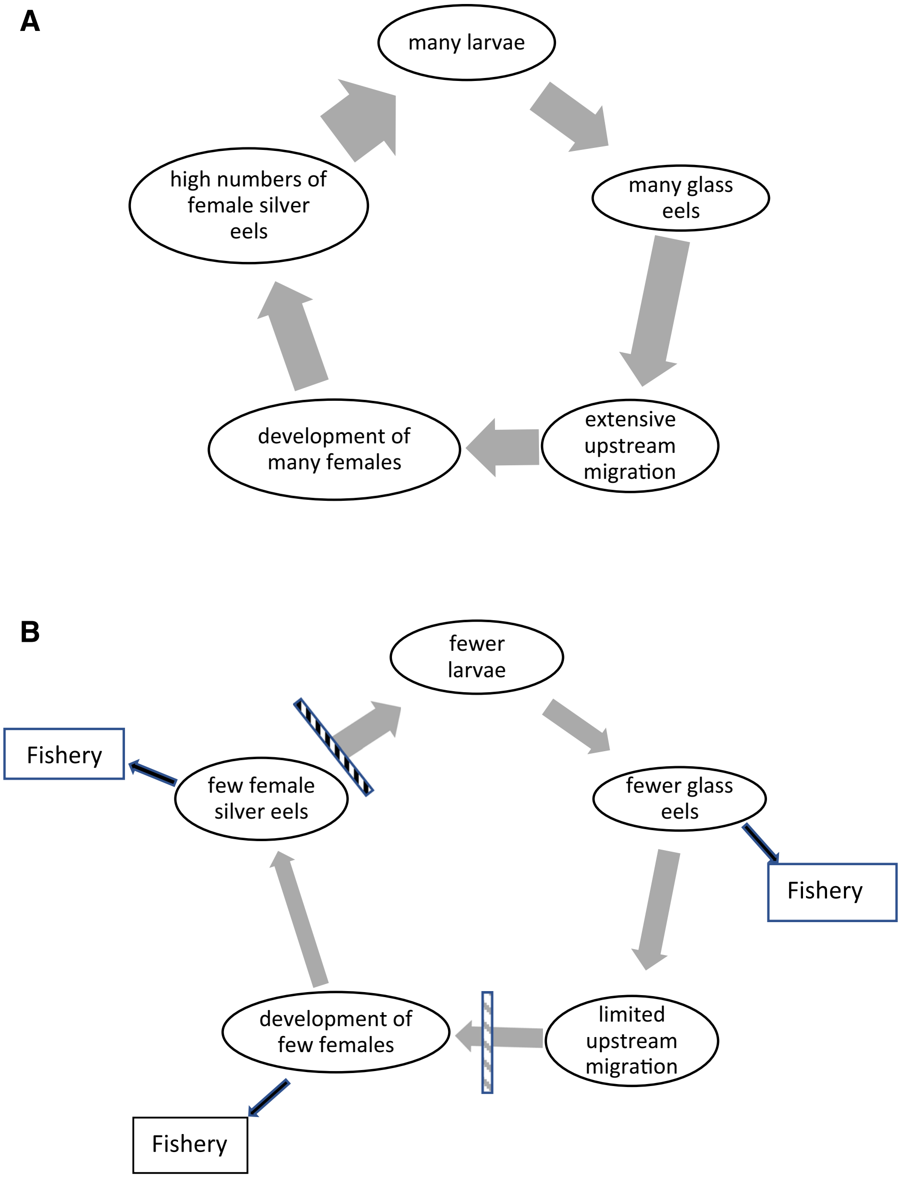

**Fig. 1** Historic (**a**) and current (**b**) life cycles of *Anguilla* spp. showing suggested impact of reduction in surplus production (thickness of cycle arrows indicates relative abundance). Hatched lines indicate barriers to migration

relatively large with a tendency to follow paths of maximum flow (Euston et al. 1998; Jansen et al. 2007), female eels are very susceptible to entrainment and injury or death when they enter turbines. Eel size typically increases with distance inland (e.g. Smogor et al. 1995) so the largest and most fecund females travel the greatest distance and are consequently exposed the greatest risks. While many structural and behavioural systems have been trialled to prevent eels entering turbines (e.g. Richkus and Dixon 2003), unfortunately there is no “silver bullet” that can be universally applied. Consequently, injury rates and mortality can be up to 100% for larger eels (Haro et al. 2000; Carr and Whoriskey 2008; Boubée et al. 2008). Although there is currently no proven stock recruitment relationship (Feunteun 2002; Aström and Dekker 2007), insufficient spawning stock biomass has been suggested as a reason for recruitment collapse (Dekker 2003).

**Table 4** Benefits and risks associated with different life history stages of *Anguilla* spp. Anthropogenic impacts in italics

| Habitat | Life history stage | Benefits | Risks |
|---|---|---|---|
| Ocean | Oceanic spawning migration | Extensive area available; diel vertical migrations reduce predation and promote maturity | Navigation; unfavourable hydrological conditions; finding a mate; predation |
| | Larval life | Extended; chance to grow; passive transport; maximise feeding opportunities and reduce predation via diel vertical migrations | Predation; entrainment in gyres; changes in oceanic circulation patterns; might miss target landfall |
| Inshore (salt, brackish, and freshwater) | Recruitment | Shoaling and nocturnal activity reduces predation; passive tidal transport reduces energy demands | Predation; restricted access via river mouth closure, *tidal gates*); *human exploitation* |
| | Juvenile upstream movement (summer) | Dispersal; encounter new habitats; benthic lifestyle reduces predation | Instream obstacles (waterfalls, *hydro*); *human exploitation;* low densities may reduce migration incentive |
| | Adult yellow eel) settlement and growth phase | Colonise preferred habitats; diverse feeding habits and opportunities; differential determination of sexes | Competition; predation; displacement by floods or water recession; *human exploitation;* longevity increases exposure to pollutants and disease; *lack of habitat connectivity* |
| | Silver eel riverine migration | Use flow (often floods) for downstream movement; pause at staging places (physiological adaptation to saline water) | Negotiate instream obstacles—waterfalls, *hydro; human exploitation* |

Over geological time scales, eel life histories have been very successful, enabling species divergence and colonisation of many landmasses. Presumably SPH played an important role in providing a numerical buffer against adverse conditions. However, today the impact of SPH is much diminished as eels face a variety of challenges to their survival within freshwater habitats. Superimposed on such challenges is variability in the marine environment, with the impacts of climate change uncertain but likely to be deleterious through lower primary productivity and changes in the strength of currents that provide larval transport (Knights 2003; Bonhommeau et al. 2008a, b; Miller et al. 2016). Irrespective of the causes, the net result has been widespread recruitment failure of several *Anguilla* spp. throughout much of the Anthropocene era.

In summary, it is proposed that the success of eels is largely due to a series of unique adaptations and life history features, of which adaptability, resilience, energetic conservatism, and environmental determination of sex are key features. It is suggested that these features have historically resulted in a significant overproduction of juveniles, and that this SPH effectively drives the eel life history as the associated high densities of juvenile eels in freshwater provide the incentive for inland penetration and the development of females. Collectively these features have been sufficient to offset the considerable risks associated with eel life histories, whether that be arrival of silver eels at often distant spawning areas and finding suitable mates, survival by larvae of an extensive marine journey, accurate navigation to arrive at continental habitats (Jellyman and Bowen 2009), survival for many years in those habitats, and eventual egress to the sea (see summary, Table 4). The present declines in recruitment of many species reduces the incentive for such density-dependant upstream migrations, and most juveniles are expected to remain in the lower reaches of waterways where the propensity for rapid initial growth and high densities will result in a high proportion of eels developing as males (Holmgren 1996; Davey and Jellyman 2005). Should recruitment decline even further, it is possible that the resulting low densities could result in an increased proportion of eels developing as females in these lower reaches, a “last-ditch’ response that may partially offset the impact of reduced recruitment.

Proving the validity of SPH may be elusive. The hypothesis is intuitive and fits with observations of vast historical recruitment but drastically reduced recruitment of many species over recent decades, and also the longitudinal distribution of sexes within catchments. However, obtaining proof could require finding correlations between the strength of glass eel recruitment and subsequent upstream migration of juveniles. Additional support could come from examining a time series of otolith microchemistry of estuarine dwelling in yellow eels where a significant increase in the extent and duration of estuarine/lower river dwelling might indicate significant changes in life history patterns associated with levels of recruitment. Studying changes in the density and proportion of female eels following dam removal would also be informative.

The SPH hypothesis underscores the importance of conservative harvest of glass eels, habitat connectivity, and the need to ensure maximum female escapement. Where extensive stocking of juvenile eels is practiced, consideration should be given to stocking areas peripheral to the main geographic locations of eels, and stocking areas well upstream where eel densities are low; both techniques should result in increased development of females, an outcome critical to the ongoing survival of the genus *Anguilla* which is currently being driven towards extinction.

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