Important questions to progress science and sustainable management of anguillid eels

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Abstract

Anguillid eels are found globally in fresh, transitional and saline waters and have played an important role in human life for centuries. The population status of several species is now of significant concern. The threats to populations include direct exploitation at different life stages, blockages to migratory routes by dams and other structures, changes in river basin management that impact habitat carrying capacity and suitability, pollution, climate change, diseases and parasites. While much has been done to understand eel biology and ecology, a major challenge is to identify the key research and management questions so that effective and targeted studies can be designed to inform conservation, management and policy. We gathered 30 experts in the field of eel biology and management to review the current state of knowledge for anguillid eel species and to identify the main topics for research. The identified research topics fell into three themes: (a) Lifecycle and Biology; (b) Impacts and (c) Management. Although tropical anguillid eels are by far the least well understood, significant knowledge gaps exist for all species. Considerable progress has been made in the last 20 years, but the status of many species remains of great concern, particularly for northern temperate species. Without improved engagement and coordination at the regional, national and international level, the situation is unlikely to improve. Further, adaptive management mechanisms to respond to developments in science, policy and our knowledge of potential threats are required to ensure the future of these important and enigmatic species.

KEYWORDS
conservation, global management, impacts, lifecycle

1 | INTRODUCTION

Anguillid eels are found across the globe except in the eastern Pacific and South Atlantic. There are currently 19 recognised species/subspecies of the genus *Anguilla*, family Anguillidae. There is huge variety in our understanding of these species, and it is recognized that more work is needed to review and synthesize existing knowledge to help develop and inform management or recovery plans, as well as to collect new information where knowledge gaps exist (Jacoby et al., 2015).

Anguillid eels exhibit a facultatively catadromous life history. Eels spawn in offshore oceanic waters, and the hatched larvae then migrate to continental waters where they feed and grow, before they migrate to an oceanic spawning area (Aoyama, 2009; Tesch, 2003). The spawning areas of both temperate and tropical anguillids (Table 1) are typically located in the open ocean (Figure 1). Common features of many of these areas include westward flowing equatorial currents, the presence of oceanographic fronts and subsurface tongues of high salinity (Schabetsberger et al., 2016). For temperate species such as the European eel (*A. anguilla)* and the American eel (*A. rostrata)*, spawning occurs far offshore, in an area extending more than 2,000 km of longitude, to the south of a strong temperature front in the Sargasso Sea (Hanel et al., 2014; Kleckner & McCleave, 1988; Miller et al., 2015, 2019; Munk et al., 2010; Schoth & Tesch, 1982), although eggs and adult *Anguilla* have never been found in the Sargasso Sea. Japanese eel (*A. japonica*) eggs and preleptocephali (Aoyama et al., 2014; Tsukamoto et al., 2011), and spawning-condition adults (Chow et al., 2009) have been found only within a narrow zone along the Pacific West Mariana Ridge seamount chain. Some species, such as the Celebes longfin eel (*A. celebesensis*, in the Celebes Sea, Tomini Bay), New Guinea eel (*A. interioris*, in the Indonesian Seas; eastern Indian Ocean) and the Australian and New Zealand shortfin eels (*A. australis* spp., in the western South Pacific) appear to spawn in multiple locations (Aoyama et al., 2003; Kuroki et al., 2006, 2020). The spawning areas of tropical anguillid eels vary more in their distances from land, with the shortfin and Pacific eel (*A. bicolor* spp.*)* spawning west of Sumatra (Jespersen, 1942), confirmed by Arai et al., (1999) and northeast of Madagascar (Robinet & Feunteun, 2002a), while the Indonesian longfinned eel (*A. borneensis)* and *A. celebesensis* spawn locally in the Indonesian Seas (Aoyama, 2009; Aoyama et al., 2018). Further integration of biological and oceanographic disciplines will continue to enhance knowledge in this area of work (e.g. Chang et al., 2020).

A critical aspect of anguillid biology relates to their physiological, behavioural and ecological adaptability. Anguillid eels share their anguilliform morphology with many other eel families, although in their larval phase, all eels have a flattened "leaf-like" leptocephalus form (Tesch, 2003). Anguillid eels show sexual dimorphism, with males generally being smaller, and maturing at a younger age, than females (Tesch, 2003). All species exhibit plasticity in habitat use, growth, maturity and morphology at all stages of the lifecycle and, in particular, during the growth phase. This means that, unlike the very specific locations of spawning areas, the distributional range of eels encompasses almost all freshwater and brackish environments and habitats, ranging from nearshore marine environments, to far inland river, stream and lake habitats across a wide range of latitudes. This is enabled by their tolerance for wide-ranging environmental conditions and by their ability to adapt to a diverse range of feeding niches (Tesch, 2003). This plasticity extends to age at maturation, with individuals of many species living for several decades and, in extreme cases, perhaps for more than a century (Jellyman, 1995). Temperature appears to be an important driver of life history: eels living in warmer environments grow faster and mature earlier (Tesch, 2003).

Not all anguillid eels are commercially important, but species such as *A. anguilla*, *A. japonica* and *A. rostrata* have been extensively harvested for food or, because it has not yet been possible to breed these species on a commercial basis, as wild stock for use in aquaculture (Musing et al., 2018). Declines in the levels of recruitment of the Northern Hemisphere temperate anguillid eels beginning in the late 1970s led to concern about the cause of these and also led to increased research of these species in recent decades (Dekker, 2003c; Dekker & Casselman, 2014). More widely, a growing number of studies on tropical eels have led to increasing concerns about the stock status of many of these species (Drouineau et al., 2018; Gollock et al., 2018), and in 2011, the IUCN Anguillid Eel Specialist Sub-Group—which became the Anguillid Eel Specialist Group in 2015—was established to assess the status of all anguillid eels. What was immediately clear was that the extent of knowledge for each species was variable, whether that related to their biology or the threats that impact them (Jacoby et al., 2015).

To focus future work most effectively, a major challenge now is to identify the most pressing issues to address to help guide the recovery of eel species. With limited financial and human resources, and some impacts being more urgent and/or easily manageable than others, there is a need to focus on the most important questions so that targeted studies can be designed to inform conservation, management and policy. To this end, 30 experts in the field of eel science attending the International Eel Symposium in London in 2017 took part in a workshop to identify the main topics relating to eel biology, ecology and management that require further knowledge. The aim of this horizon scanning exercise was to review existing knowledge and identify future priorities, including the need to inform management measures that will help to guide a well-informed research agenda and meet both national and international sustainability and conservation commitments such as the EU Biodiversity Strategy (EU, 2020), CITES and CMS listings (CITES, 2020a,b), and IUCN Recommendations (IUCN, 2016).

TABLE 1 List of the 19 species/subspecies of anguillid eels, organized in order of species complex (Aoyama, 2009)

Latin name	Common name	Distribution	L_{max} (cm)	IUCN status
A. celebesensis Kaup, 1856	Celebes longfin	Tropical	150	Data Deficient
A. interioris Whitley, 1938	New Guinea	Tropical	80	Data Deficient
A. megastoma Kaup, 1856	Pacific longfin	Tropical	165	Data Deficient
A. luzonensis Watanabe, Aoyama & Tsukamoto, 2009	Philippine mottled	Tropical	100	Vulnerable
A. bengalensis bengalensis Gray, 1831	Indian mottled	Tropical	200	Near Threatened[a]
A. bengalensis labiata Peters, 1852	African mottled	Tropical	175	Near Threatened[a]
A. marmorata Quoy and Gaimard, 1824	Giant mottled	Tropical	200	Least Concern
A. reinhardtii Steindachner 1867	Australian longfin	Tropical	165	Least Concern
A. borneensis Popta, 1924	Indonesian longfinned	Tropical	Not known	Vulnerable
A. japonica Temminck and Schlegel, 1846	Japanese	Subtropical/temperate	150	Endangered
A. rostrata Lesueur, 1817	American	Subtropical/temperate	152	Endangered[b]
A. anguilla Linnaeus, 1758	European	Temperate	133	Critically Endangered
A. dieffenbachii Gray, 1842	New Zealand longfin	Temperate	185	Endangered
A. mossambica Peters, 1852	African longfin	Tropical	150	Near Threatened
A. bicolor bicolor McClelland, 1844	Shortfin	Tropical	80	Near Threatened[a]
A. bicolor pacifica Schmidt, 1928	Pacific	Tropical	123	Near Threatened[a]
A. obscura Günther, 1872	Pacific shortfin	Tropical	110	Data deficient
A. australis australis Richardson, 1841	Australian shortfin	Subtropical/temperate	130	Near Threatened[a]
A. australis schmidtii Phillipps, 1925	New Zealand shortfin	Subtropical/temperate	130	Near Threatened[a]

Note: The common names follow those recently proposed by Tsukamoto et al. (2020). Total length data are predominantly taken from FishBase (https://www.fishbase.se/), except *A. bicolor bicolor* (Skelton, 2001). All Red List assessments were updated in 2019–2020 except *Anguilla rostrata* ([b]2013 to be updated in 2021). Subspecies are not assessed under the Red List Categories and Criteria, and status therefore refers only to the species level (marked by[a]).

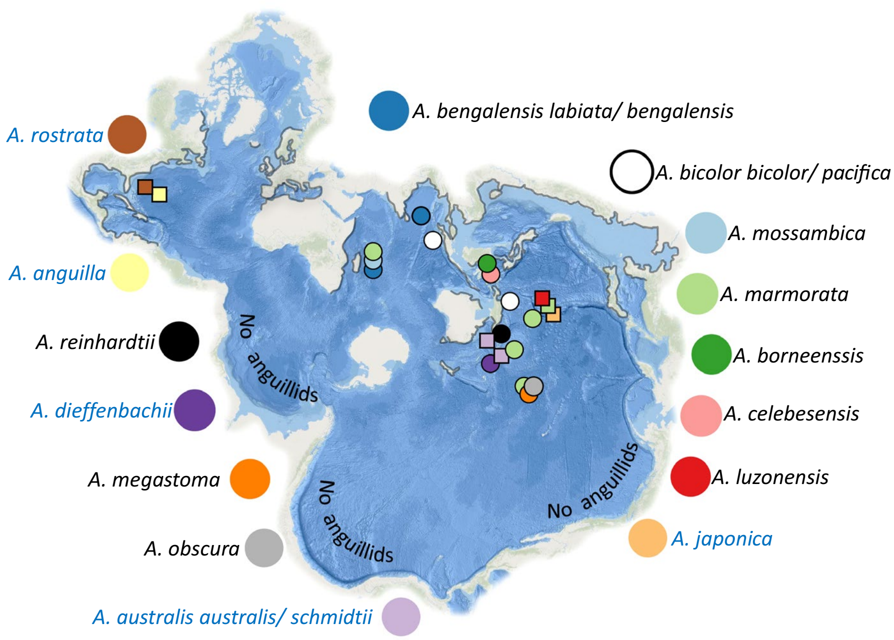

FIGURE 1 Map of known and estimated spawning areas of anguillid eels based on existing information for temperate (names in blue) and tropical species. The coastlines of the growth habitat and spawning areas are adapted from Miller and Tsukamoto (2017). Known and estimated spawning are shown by squares and circles respectively. Known spawning areas are based mainly on larval catches, and estimated spawning areas are based on various types of information, including limited larval catches, evidence about population structure (including hybridization), pop-up tagging studies on silver eels, or species ranges in relation to ocean current patterns. Since the estimated locations of a number spawning areas are very uncertain the map is designed to be illustrative of existing knowledge. *Anguilla interioris* is not shown but likely spawns locally in the Indonesia Seas region. The map is presented in the Spilhaus projection, which highlights the oceans and the oceanic distribution of spawning locations rather than the position and size of the continental landmasses. This figure is only available to view in colour in the online version

2 | METHODS

We used the common procedure (e.g. Sutherland et al., 2013), of bringing together experts in the field, soliciting their views about the most important research or management questions, compiling and identifying those questions from the replies received and then reaching consensus on the final list by way of a vote. The process began with a survey of experts who were planning to attend or who

TABLE 2 Topic review, important research questions and their impact

	Topic	Main questions	Impact
Theme 1	Larval ecology	Swimming behaviour Sensory biology Growth rates	Drift modelling Orientation and navigation Stock–recruitment
	Glass eel recruitment	Environmental drivers Settling patterns/habitat selection Fisheries mortality	Stock–recruitment Population modelling Management measures
	Genetic structure	Panmixia Within-generation selection Genomics	Population resilience Local adaptation & life-history characteristics Screening for impacts
	Habitat and productivity	Fine-scale habitat mapping Habitat enhancement Seasonal changes	Population distribution Management measures Survey techniques
	Diet and foraging	Diets of estuarine eels Tropical eel diets Competition & overlap	Stock assessment Ecological role Carrying capacity
	Marine and brackish eels	Contribution to spawning stock Life-history strategies Population trends	Stock assessment Population structure Stock assessment
	Oceanic migration	Spawning behaviour Vertical migrations Migration success	Spawning success Predation risk Population resilience
	Reproduction	Environmental variability Spawning aggregations Spawning potential	Spawning area location Effective population size Stock–recruitment
Theme 2	Climate	Influence on larval survival Effect on life history Extreme weather, including drought	Recruitment success Population structure Natural mortality
	Hydropower	Impact on migration Habitat alteration Direct mortality	Escapement success Population structure Management measures
	Pollution	Cumulative impacts Chronic effects Reduced reproductive potential	Anthropogenic mortality Population resilience Stock assessment
	Effect of parasites	Parasite loads Impacts on ocean migration Cumulative impacts	Natural mortality Stock assessment Mortality
	Fisheries	Exploitation rates Multiple effects Design of management measures	Stock assessment Stock assessment Population recovery
Theme 3	Stock assessment	Abundance time series Stock–recruit relationship Standardization	Data-rich assessment Population modelling Quantifying uncertainty
	Effective management	Data collection International collaboration Evaluation	Standardization Success of measures Improved measures
	Stocking eels	Effectiveness Transmission of disease/parasites Migration failure	Management measures Natural mortality Stock assessment
	Aquaculture	Maturation of adults Food production Survival of leptocephali	Increased choice of broodstock Increased survival of leptocephali Production costs reduced
	Trade	Scale of exports Illegal trade Pressure on tropical species	Use of exports Design of measures Management measures

had submitted papers to the International Eel Symposium in London in 2017. They were each asked to identify 10 questions in eel science and/or management that they considered of greatest importance. Where similar questions were received, they were combined into a single question. These questions were then compiled and grouped under general headings. The full list of questions was distributed and the participants were asked to vote on their top 10 questions. The votes were tallied, a final list of key questions was circulated, and the 20 most important questions were discussed and agreed on at a workshop organized after the final day of the symposium (16 June 2017). Following the write-up of the workshop, the participants were asked to confirm they agreed with the re-articulation of questions and the topics they encompassed (Table 2). The list was finalized and the manuscript written with input from all participants, including a survey of the state of knowledge of the topics covered. The topics are all considered to be important, and the order they are presented does not indicate a ranking.

3 | RESULTS

3.1 | Theme 1: Lifecycle and biology

3.1.1 | How do larval eels migrate from spawning areas to the continental growth habitat?

The first spawning area of anguillid eels was discovered to be in the Sargasso Sea, based on the collection of small eel larvae—called leptocephali—of the Atlantic eels there, which became a widely known example of a long-distance fish spawning migration (Schmidt, 1923a, 1923b). Based on collections of leptocephali during oceanographic sampling surveys across several ocean basins, the spawning areas of both temperate and tropical anguillids have been located in the open ocean, tens to thousands of kilometres offshore from their continental growth habitats (Aoyama, 2009; Miller & Tsukamoto, 2017; Schabetsberger et al., 2016). Leptocephali are transparent and laterally compressed (Miller, 2009), with bands of muscle that enable undulatory swimming and well-developed eyes and olfactory organs (Hulet, 1978). Leptocephali are, therefore, well equipped for both passive and active swimming during their oceanic migration (Chang et al., 2018; Kuroki et al., 2020; Miller & Tsukamoto, 2017). This larval form is notably larger than that of almost all other fish species—leptocephali typically reach a maximum length ~ 55–90 mm (Kuroki et al., 2014; Miller & Tsukamoto, 2017)—and their morphology and capabilities are thought to enable trans-oceanic drift of up to several years.

The conventional picture of the larval migration, proposed by Schmidt (1923a), is based on the studies of *A. anguilla*, with a extended period between hatching and eventual arrival at a distant continental shelf, the location of which is determined in large part by the predominant ocean currents. For temperate species, this paradigm is borne out by a lack of intraspecific genetic differentiation and a wide distribution. However, analyses of otolith daily rings in some species indicate the potential for much faster movement (Kuroki et al., 2014; Lecomte-Finiger, 1992; Réveillac et al., 2008). The reason for the discrepancy is unclear (Bonhommeau et al., 2010) but, because of the difficulties of studying the behaviour of individual leptocephali in the ocean, little is known about how well they swim and the relationship between larval transport and recruitment is not fully understood (Miller, 2009; Miller & Tsukamoto, 2017). It may be possible that, alongside developments in the field study of leptocephali, further behavioural or physiological studies (e.g. Yamada et al., 2009) can be conducted with artificially spawned and reared leptocephali that will elucidate the swimming capabilities and migration ecology of anguillid eel larvae. Early life-history studies based on microstructure and microchemistry (trace elements and isotope ratios) of otoliths of leptocephali and glass eels collected along the distribution ranges of different eel species may also give insights on the environmental characteristics of spawning areas and the journey to the growth habitat (Kuroki et al., 2014; Martin et al., 2010; Réveillac et al., 2008).

3.1.2 | What factors influence the strength and distribution of glass eel recruitment?

Significant declines in glass eel recruitment have been observed for many anguillid species, with most attention having been focused on the severe reductions since the 1970s in the three north temperate species: *A. anguilla*, *A. rostrata* and *A. japonica* (Dekker & Casselman, 2014). Long recruitment time series for other species have not been collected, although a limited recruitment data set from the early 1970s and early 2000s shows a decreasing trend in both New Zealand longfin eel (*A. dieffenbachii)* and *A. australis* in New Zealand (Jellyman et al., 2009). No direct cause and effect relationships have been demonstrated, but there are two primary, synergistic, hypotheses for the declines: reduced effective spawning stock biomass and quality (ICES, 2017) and/or reduced larval survival and quality. The former has been attributed largely to fishing, contamination by anthropogenic pollutants, habitat loss, habitat fragmentation or degradation (i.e. the continental phase), while fluctuations in larval survival are thought to be due to changing oceanic conditions (Kim et al., 2007; Kimura et al., 2001; Miller et al., 2016; Miller, Kimura, et al., 2009; Westerberg, Pacariz, et al., 2018) or low spawner or egg quality (see section 3.2.3 "How does pollution affect the viability of eel stocks?").

The mechanisms that underpin the recruitment of glass eels to continental habitats are not well understood, particularly in tropical anguillid species (Cresci, 2020; Helme et al., 2018; Hewavitharane et al., 2018), but are known to include physiological as well as environmental drivers that can act over timescales of days to weeks (Edeline et al., 2009; review by Harrison et al., 2014). Glass eel and leptocephalus mortality, be it natural or due to anthropogenic activities, is particularly poorly understood and in need of further research to enable sustainable management (e.g. ASMFC, 2017; Dekker, 2002; Drouineau et al., 2016). The relationship between population size and larval production and mortality, the stock–recruitment relationship, is poorly understood in all species of anguillid eels due to the complex life history of these species. More research on the factors governing the survival and behaviour of leptocephali will contribute to a better understanding of the relationship between the dynamics of the larval stage and recruitment success, which is particularly true for species that spawn sympatrically and/or in very distant areas (Miller & Tsukamoto, 2017).

3.1.3 | How are eel stocks genetically structured?

Schmidt (1923b) originally proposed that the single spawning area in the Sargasso Sea was strong evidence of panmixia in *A. anguilla*, a life-history paradigm that has since been assumed for most other anguillid species (Tesch, 2003). Although Schmidt's assertion for *A. anguilla* has been challenged (Baltazar-Soares et al., 2014; Maes & Volckaert, 2007; Tucker, 1959; Wirth & Bernatchez, 2003), recent genetic work has supported Schmidt's original hypothesis. For example, Als et al. (2011) genotyped over 1,000 *A. anguilla*, including larvae from the Sargasso Sea, at 21 microsatellite loci. There was low, nonsignificant genetic differentiation among a total of 21 geographical and temporal samples from across Europe. Similarly, Pujolar et al., (2014) found no genetic differentiation among locations after analysing 453,062 single nucleotide polymorphisms in *A. anguilla* glass eels captured from eight locations across a broad geographic area. Côté et al., (2013) genotyped over 2,000 *A. rostrata* from 12 cohorts using 18 microsatellite loci and found no genetic differences among sampling sites or between life stages. Han et al., (2010) assessed over 1700 *A. japonica* from 31 spatial and temporal replicates at eight microsatellite loci and found no evidence for genetic structuring. There is, however, at least one case that highlights panmixia is not universal; the giant mottled eel (*A. marmorata)* appears to have four spawning populations (North Pacific, South Pacific, Indian Ocean and Guam) based on mitochondrial and microsatellite analyses (Minegishi et al., 2008). Similar results have been observed in *A. australis*, where genetic differences in five microsatellite loci were observed between geographically isolated populations, suggestive of either different spawning populations or subspecies of New Zealand and Australian residents (Shen & Tzeng, 2007). The geographical distribution of *A. bicolor* in both Indian and Pacific basins indicates this species may also have multiple spawning sites. Understanding panmixia and the mechanisms that underpin any genetic structuring of eel populations is fundamental to the management of eel populations and the development of integrated demographic-genetic models (Jacobsen et al., 2018; Mateo et al., 2017; Pujolar & Maes, 2016).

When different eel species share spawning locations, they have great potential for interspecies mating (Avise et al., 1990). Using genomic data, frequent occurrence of hybridization has been demonstrated for the two Atlantic *Anguilla* species (*A. anguilla* and *A. rostrata*) (Albert et al., 2006; Gagnaire et al., 2011; Pujolar & Maes, 2016; Wielgoss et al., 2014), as well as several tropical eel species (Barth et al., 2020; Schabetsberger et al., 2015). In an extensive genomic analysis of species throughout the Indo-Pacific, hybrids for *A. marmorata* with the Pacific longfin eel (*A. megastoma)*, Pacific shortfin eel (*A. obscura)* and *A. interioris*, as well as *A. megastoma* with *A. obscura* were found. However, cytonuclear incompatibilities, hybrid breakdown and purifying selection support species cohesion even when hybridization has been pervasive throughout the evolutionary history of clades (Barth et al., 2020). The fact that eel species sometimes interbreed makes them good model organisms for the study of hybridization in migratory marine fish, and more broadly, the biological and evolutionary implications of this.

The application of recent advances in genetic screening enables the examination of genomes for possible within-generation adaptation. To date, studies on *A. anguilla* and *A. rostrata* have identified genetic differences in eels residing in different habitats (Pavey et al., 2015) and across broad geographic areas (Gagnaire et al., 2012; Pujolar et al., 2014). These variations have included genes with a role in metabolism, circadian rhythm and calcium ion regulation. Although genetic mixing due to panmixia will limit the evolutionary impact and development of these adaptations, they provide an explanation for differences in life-history characteristics at different geographic locations. For example, Laporte et al., (2016) demonstrated that *A. anguilla* and *A. rostrata* exhibited genetic differences that were related to the level of pollution at sampling sites. This has implications for the success of glass eel stocking strategies and suggests that a better understanding of the importance of local genetic adaptations and their role in expression of life-history characteristics is urgently required (Pavey et al., 2015) so that the most effective management strategies can be developed.

3.1.4 | What factors influence habitat use and productivity of eel stocks?

Anguillid eels are habitat generalists and can use a variety of aquatic realms through their complex lifecycle, including oceanic waters, continental shelves, estuaries and freshwater environments (Tesch, 2003). Such habitat flexibility facilitates their broad intra- and interspecific distributions (Helfman et al., 1987); however, they also demonstrate specific microhabitat preferences and requirements. Factors driving habitat selection include water depth, temperature, salinity, substrate, water velocity, oxygen concentration, vegetation cover and biotic features such as prey availability, threat of predation and the presence of other eels (Greene et al., 2009; Jellyman & Arai, 2016; Laffaille et al., 2003, 2004; Steele et al., 2018). Knowledge of tropical anguillid habitat use is more limited than for temperate eels (Arai & Abdul Kadir, 2017). However, the mechanisms governing distribution are likely to be complex: tropical species often coexist within catchments but occupy different habitats due, in part, to different interspecific preferences. Therefore, in rivers in French Polynesia, *A. obscura* predominate in estuaries, *A. marmorata* in middle reaches and *A. megastoma* in upper reaches (Marquet & Galzin, 1991).

Habitat associations change with ontogenetic stage, prey availability, temperature and physiology. In continental waters, small eels exhibit stronger habitat selection than larger eels, favouring low water velocity and depth (Jellyman & Arai, 2016; Laffaille et al., 2004) with abundant cover (Lloyst et al., 2015). Seasonal shifts in habitat use are well documented for yellow eels in temperate regions, for example, their selection of different types of cover and substrate in summer (Lloyst et al., 2015; Ovidio et al., 2013) and winter (Tomie et al., 2017). Seasonal movements between freshwater and estuarine habitats by *A. rostrata* take advantage of higher productivity in brackish water and better overwinter survival in freshwater, accelerating growth, maturity, and out-migration (Pratt et al., 2014). Wiley et al., (2004) identified the main predictors of riverine eel density to be water velocity and depth, distance inland, density of other fish species and distance to semipassable or impassable barriers.

Habitat loss, modification and access are major threats to anguillid eels (Haro et al., 2000; Jacoby et al., 2015). Understanding fine-scale habitat use is fundamental and advanced GIS mapping is essential if habitat is to be quantified, evaluated, and protected (Cairns et al., 2012). For example, Chen et al., (2014) used chronological Landsat imagery from the 1970s to 2010s to assess Japanese eel habitat reductions in 16 rivers in Asia. More information and synthesis on the impacts of habitat enhancement and the effects of habitat modification (e.g. revetment alterations, Itakura et al., 2015; marsh reclamation, Laffaille et al., 2004) would be informative. Specific sampling techniques are required to locate eels and describe their microhabitat and density, such as GPS-integrated electrofishing and enclosure sampling (Claus & Malte, 2015). Increasingly sophisticated telemetry (temperature, depth, salinity, activity) and otolith topographic microchemistry (e.g. Sr, Ba, δ13C, δ18O) can reveal precise details on habitat use, requirements, and migrations (Benchetrit et al., 2017; Starrs et al., 2016). Because they have strong management implications, the effect of eel density on a number of important behavioural and life-history characteristics is key, such as movements and related habitat preferences (Feunteun, 2002), survival (Boulenger, Acou, et al., 2016), growth (Boulenger, Crivelli, et al., 2016) and sex determination (Costa et al., 2008). These, and other factors, make the modelling of eel production and carrying capacity (Acou et al., 2011) a critical component of any watershed management plan.

3.1.5 | How does eel diet and foraging strategy vary temporally and geographically?

Diet and foraging studies have mostly focused on the growth (or yellow eel) stage (Cairns, 1950; Dörner & Berg, 2016; Tesch, 2003), hence knowledge on the feeding ecology of both the leptocephalus and glass eel stages remains limited (Miller et al., 2020). Silver eels do not feed, based on studies that show the gut loses its ability to absorb food during the silvering process (Durif et al., 2005; Pankhurst & Sorensen, 1984). For leptocephali, the presence of large, thin, forward-pointing teeth likely reflects consumption of large, soft objects such as marine snow particles including discarded appendicularian houses or gelatinous pellets (Miller et al., 2019; Mochioka & Iwamizu, 1996; Tsukamoto et al., 2013; Westerberg, 1990), although DNA sequencing studies suggest many types of materials aggregate into those consumed (Ayala et al., 2018; Chow et al., 2019; Riemann et al., 2010). Feeding does not occur during metamorphosis from leptocephalus to glass eel and during the early glass eel stage, when individuals rely on energy accumulated as leptocephali (Miller, 2009; Okamura et al., 2012; Tesch, 2003). Once feeding commences, *A. anguilla* glass eels continue to consume marine food items (Bardonnet & Riera, 2005), then switch to benthic feeding once they reach coastal waters (Tesch, 2003) where food items are diverse and seasonally dependent (Belpaire et al., 1992; Tesch, 2003).

Yellow eels are opportunistic benthos feeders, with consistent patterns among *A. anguilla*, *A. rostrata*, *A. dieffenbachii* and *A. australis*. Aquatic insect larvae of the Trichoptera and Ephemeroptera are the predominant food sources in running waters, whereas chironomids, molluscs, fish and crayfish are more important in lakes (Dörner & Berg, 2016). In saline/brackish waters, crustaceans, fish and amphipods constitute the main food items (Dörner & Berg, 2016; Tesch, 2003), which is also the case for *A. japonica* (Kaifu et al., 2013). Differences in eel feeding intensity and habits can largely be attributed to the availability of different prey taxa in the benthic communities (Dörner & Berg, 2016; Kaifu, Miyazaki, et al., 2013). The feeding ecology of some tropical species remains almost completely unknown (Dörner & Berg, 2016).

Increased knowledge about feeding of the leptocephalus and first feeding stages is relevant to aquaculture, but also to determine whether density-dependent larval starvation may occur during low ocean productivity events (Miller et al., 2016). Given the assumed dependence of leptocephali on marine snow related particles, the impact of ubiquitous microplastic pollution throughout the world's oceans (Clark et al., 2016), is also a key concern about which almost nothing is known.

3.1.6 | What proportion of eels live in saline waters, and how important are they to the stock?

Anguillid eels appear to show a high degree of plasticity regarding their dependency on freshwater habitats, as demonstrated by studies that used techniques such as otolith microchemistry and stable isotope ratio to assess habitat occupancy (Arai et al., 2004; Chino & Arai, 2010; Clément et al., 2014; Harrod et al., 2005; Jessop et al., 2002; Kawakami et al., 1998; Lin et al., 2015; Shiao et al., 2003; Sjöberg et al., 2017; Tsukamoto & Arai, 2001; Tzeng et al., 2007; Yokouchi et al., 2011). These indicate that some eels exhibit "classical" catadromy, entering freshwater systems to feed and grow but that there is a significant proportion that remains in transitional waters and/or coastal habitats, and others that migrate between differing salinities (Cairns et al., 2004; Daverat et al., 2006; Tsukamoto et al., 1998; Tzeng et al., 2000). Recent studies suggest that habitat choice or occupation may be related to genotype (e.g. Pavey et al., 2015), but it is clear that eels exhibit a broad facultative, rather than obligate, catadromy. In general, the growth of yellow eels in estuaries appears to be faster than in freshwater habitats which may confer a benefit to these individuals (e.g. Jessop et al., 2002; Kaifu, Miller, et al., 2013; Melià et al., 2006; Walsh et al., 2006; Yokouchi et al., 2008), but the full range of proximate and ultimate drivers for the observed variance in catadromy is not fully understood. This variance has a practical significance; the difficulties of assessing the abundance or biomass of eels in coastal and estuarine habitats means that determining the proportion of saline water eels within stocks and species, and their contribution to the spawning stock, remains a considerable challenge. Data from both *A. anguilla* and *A. japonica* silver eels has shown that brackish and/or marine waters are home to significant numbers of silver eels (Amilhat et al., 2008; Kotake et al., 2005; Tsukamoto et al., 2009), but much more work is needed to determine the proportion that has spent their entire life in marine environments. Overall, studies of the ecological role of eels living in marine habitats, and the extent to which trends in abundance of the marine resident mirrors those in freshwater, are still at an early stage, and this will be an important area for future research.

3.1.7 | How do eels migrate across the ocean to spawn?

The longer migrations of temperate anguillids likely evolved from shorter migrations similar to those of the tropical anguillids in the Indo-Pacific (Table 1; Kuroki et al., 2014). Direct studies on the migrations of eels became possible with the advent of acoustic tracking technology in the 1960s. These provided information on swimming directions and speeds (Aoyama et al., 1999; Fricke & Kaese, 1995; McCleave & Arnold, 1999; Tesch, 1978; Westerberg, 1979). More recent pop-up archival transmitting tags offer the major advantage of long-term remote data collection to help determine migration routes and spawning locations. The first use of these tags was with female *A. dieffenbacchi* (Jellyman & Tsukamoto, 2002) and studies on other species have followed (*A. anguilla* Aarestrup et al., 2009; Amilhat et al., 2016; Righton et al., 2016; *A. japonica* Chow et al., 2015; Manabe et al., 2011; *A. megastoma*, *A. marmorata* Schabetsberger et al., 2013; *A. rostrata* Béguer-Pon et al., 2015). None of the studies have tracked eels to their spawning areas, though some have mapped their migrations across thousands of km (Righton et al., 2016), and been very close to, or within, known spawning areas (Béguer-Pon et al., 2015; Schabetsberger et al., 2015).

One important feature of the spawning migrations of anguillid eels reported in these studies is the repeated, but so far only partly explained occurrence of significant daily vertical migrations (DVM). Eels reside in very deep water during the day (between about 600 and 900 m) and move into shallower water during night-time (between about 100 and 300 m) (Chang et al., 2020; Manabe et al., 2011; Righton et al., 2016; Schabetsberger et al., 2016), sometimes over temperature ranges of up to 20°C. The occupation of deep water during the day is generally accepted to be an anti-predator behaviour with a strong link to illumination (Jellyman & Tsukamoto, 2010; Righton et al., 2016; Schabetsberger et al., 2016; Wu et al., 2018). However, since silver eels do not feed, the function of the vertical migration into shallower water has so far been suggested to be related to thermal regulation and control of maturation (Aarestrup et al., 2009; Béguer-Pon et al., 2017; Jellyman & Tsukamoto, 2010), but the relative importance of these factors during DVM have not been determined.

To date, the primary focus of migration studies has been the gathering of information on routes, timing and/or behaviour of the better-understood species. All studies of oceanic migration have been made on females due to the fact that the satellite tags, at present, are still too large to deploy on male eels. As the field matures, more integrated studies that develop estimates of the proportion of eels that migrate successfully to spawn, and the factors that contribute to this, such as predation pressure, spawner quality and the impacts of parasites and disease, will be possible (Righton et al., 2016).

3.1.8 | What factors influence reproductive success?

The approximate oceanic spawning locations of anguillid eels have been at least generally estimated for all temperate and many tropical species (Figure 1). Knowing the locations of spawning areas is an important first step for understanding life histories and population dynamics, simply because the reproductive success of adults and eventual recruitment of glass eels are influenced by the characteristics of these locations. Very few post-spawning eels have been caught except for a small number of *A. japonica* and *A. marmorata* specimens caught in the Pacific Ocean (Tsukamoto et al., 2011), which confirmed hypotheses relating to their batch spawning and lunar cyclicity. Beyond this, almost nothing is understood about the reproductive or energetic status of eels at spawning areas. Laboratory studies have provided observations of the artificial maturation and spawning of *A. anguilla* (Boetius & Boetius, 1980; Mordenti et al., 2013), suggesting that maturation of gonads occurs over a lengthy period (five to six months). Other studies have provided analysis of energy use during sustained swimming (van den Thillart et al., 2004) that showed eels are very efficient swimmers under controlled conditions. Even so, considering the physical and physiological constraints of ocean migration, it seems likely that eels do not return to the continental habitat, and instead, they die after spawning (i.e. are semelparous). Improved knowledge of spawning locations and the oceanographic processes that define them will increase the potential to use hydroacoustics, underwater cameras and submersibles to identify spawning aggregations of adults, and enable the testing of this and other hypotheses. This has, so far, been attempted for *A. japonica* (Fukuba et al., 2015; Tsukamoto et al., 2013), with promising early results. If spawning events can be identified, either directly or through modern genetic and molecular methods such as eDNA (Takeuchi et al., 2019), information about the number of spawners, sex ratios, courtship behaviour etc., will be obtained.

Understanding these factors will provide a better understanding of the evolutionary aspects of why and how eels aggregate and spawn in the ocean, contributing to both effective management and aquaculture. More broadly, considering the range of impacts that may affect eels' ability to migrate—particularly those that can affect spawner quality, such as pollution, parasites and disease and resource limitation (Freese et al., 2017, 2019; Palstra et al., 2007; Sühring et al., 2015)—also see the Sections below relating to pollutants, and parasites and diseases—it is essential that we understand better how spawner quality, and not just spawner biomass, affects population sustainability.

3.2 | Theme 2: Impacts

3.2.1 | What might be the effects of climate change on eel stock dynamics?

Climate change impacts diadromous fishes across their range (Hare et al., 2016; Reist et al., 2006) and is considered to be one of the least understood threats to anguillids globally (Jacoby et al., 2015). The global decline of eel abundances suggests that common factors may, at least in part, be responsible (Bonhommeau et al., 2008; Friedland et al., 2007; Knights, 2003). While any effects of climate change will likely influence eels at every life-stage, the impact is arguably greatest in the larval phase (Díaz et al., 2018) through changes to currents, growth rates and food availability. For example, *A. anguilla* glass eel recruitment is negatively correlated with the North Atlantic Oscillation (Arribas et al., 2012; Castonguay, Hodson, Moriarty, et al., 1994; Dekker, 2004; Friedland et al., 2007; Kettle et al., 2008; Knights, 2003; Miller et al., 2016) as well as sea surface temperature (Bonhommeau et al., 2008; Durif et al., 2010; Gutiérrez-Estrada & Pulido-Calvo, 2015). These general patterns are supported by other studies; recruitment of *A. anguilla* has been shown to be positively correlated with primary production and temperature in the Sargasso Sea (Arribas et al., 2012; Bonhommeau et al., 2008); variations in atmospherically driven ocean currents in the Sargasso Sea have been identified as a driver of the sharp decline in *A. anguilla* recruitment at the beginning of the 1980s (Baltazar-Soares et al., 2014). These effects may be amplified by reductions in larval production: simulations of larval drift from the spawning area to the eastern North Atlantic (Pacariz et al., 2014) and a later study (Hanel et al., 2014) showed that *A. anguilla* and *A. rostrata* larval abundance in the Sargasso Sea in 2011 was approximately an order of magnitude lower compared to the period of 1983 and 1985, during the onset of the recruitment decline (Westerberg, Miller, et al., 2018). It is important to note that these studies are inferential rather than empirical; at present, there is no direct evidence of climate influences on eel stock dynamics. Further, the majority of studies have primarily focussed on *A. anguilla* and a critical evidence gap is understanding the impacts of changing climate on all eel species.

Predicting the influence of climate-induced impacts in the continental habitat is complex because responses will vary with species, habitat, geography and the impact of other threats. The broad distribution of temperate anguillids includes areas that are below the optimum temperature for growth (Dekker, 2003b) and predicted rises in river or lacustrine temperature might increase eel growth and shorten generation time. However, this effect might then be attenuated by decreases in river flow and increases in the frequency, duration and severity of meteorological and hydrological droughts in temperate areas (Baptista et al., 2010; Otero et al., 2011). Gaining a greater understanding of the interaction between environment and life-history response in eels, particularly tropical species, will be critical to building effective forecasts into stock assessment and management, and adapting conservation goals and actions.

3.2.2 | What is the effect of dams and hydropower facilities on eel stocks?

Hydroelectric power (HEP) is the largest renewable energy resource globally, accounting for an estimated 15.9% of generation in 2019 (REN21, 2020). More than 8,600 HEP dams (>1 MW in capacity) are currently in operation worldwide, with a further 3,682 either under construction or planned (Zarfl et al., 2015, 2019). Dams may delay or prevent the immigration of juvenile eels, rendering upstream habitats inaccessible. For seaward-migrating adults, HEP facilities cause sublethal damage (Bruijs & Durif, 2009) and direct mortality (Calles et al., 2010; Pedersen et al., 2012) as well as migration delay or failure (Besson et al., 2016; Trancart, Feunteun, et al., 2018; Trancart, Tétard, et al., 2018). Eels are particularly vulnerable at screens and turbines due to their elongated morphology and poor burst swimming capabilities (Boubee & Williams, 2006; Calles et al., 2010; Russon et al., 2010). In heavily impacted rivers, the cumulative effect of multiple structures may reduce overall escapement to a level below the relevant conservation targets (Breteler et al., 2007; Pedersen et al., 2012), for example the 40% escapement target for silver eels in EU countries. Connectivity can be partially restored at obstructions through technical solutions. "Eel ladders" that aid upstream migration are widespread across Europe, North America and New Zealand, although there are few quantitative assessments of their efficiency (Jellyman & Arai, 2016). For adult downstream migration, efforts have focused on preventing turbine entry, using physical screens and/or behavioural guidance technologies (Calles et al., 2013; Piper et al., 2019).

Despite the research effort to date, identification of the best technologies to reduce the impacts of HEP remains challenging. For example, observations on the response of *A. anguilla* to infrasound initially showed promise (Sand et al., 2000), but only limited benefits have been demonstrated in subsequent field tests (Baran et al., 2012; MacNamara, 2012; Piper et al., 2019). Similarly, the observed deflection of silver eels at light arrays (Cullen & McCarthy, 2000; Hadderingh et al., 1992) offers only limited applicability in turbid water. Adult passes using surface or undershot routes have shown typically lower than expected efficiencies (Gosset et al., 2005;

Legault et al., 2003; Travade et al., 2010). Alternative "trap and transport" approaches that capture eels and transfer them downstream of obstructions are used in Europe, North America and New Zealand (Béguer-Pon et al., 2018; ICES, 2016a; Jellyman & Unwin, 2017). Altered management regimes such as generation-stoppages and enhanced weir spillage during migration peaks may be effective (e.g. Boubee et al., 2001; Trancart et al., 2013), but can be costly and logistically complicated unless they are clearly forecasted to limit economical loss (Teichert et al., 2020).

As is typical, most research has focused on protection and passage of *A. rostrata*, *A. anguilla*, *A. australis* and *A. dieffenbachii*, so the impact of HEP on *A. japonica* and tropical species is virtually unknown. HEP impacts on eels within East Asia and the Indo-Pacific have received little attention and provision of safe passage of downstream migrants of all species remains largely unresolved.

3.2.3 | How does pollution affect the viability of eel stocks?

The pollutant burden in eels has been extensively reported for both *A. anguilla* (Belpaire & Goemans, 2007; Dekker, 2016; Geeraerts & Belpaire, 2010; ICES, 2012; Robinet & Feunteun, 2002b) and *A. rostrata* (Ashley et al., 2007; Hodson et al., 1994). A wide variety of chemical contaminants have been reported in eel tissues, often at very high levels. Even within small geographic ranges, the level of contamination may vary by up to four orders of magnitude (see Belpaire et al., 2016; Freese et al., 2016, for examples). Only in areas with very low environmental impacts (such as Norway, Holmqvist et al., 2006; and Scotland, Oliver et al., 2015) can eels be expected to exhibit low pollutant burdens (Bourillon et al., 2020). Despite the extensive literature on *A. rostrata* and *A. anguilla*, there are still only a few studies on the chemical contamination of other species of eels (Arai et al., 2012; Arai & Takeda, 2012; Calvi et al., 2006; Holmqvist et al., 2006; Khalil et al., 2017; Le et al., 2010; Ohji et al., 2006; Redmayne et al., 2000; Yamamuro et al., 2019).

Pollution has been implicated as a contributing cause of the decline of *A. anguilla* and *A. rostrata* (e.g. Belpaire, 2008; Byer, 2013; Castonguay, Hodson, Couillard, et al., 1994; Geeraerts et al., 2011; ICES, 2016b; Palstra et al., 2006; Robinet & Feunteun, 2002b; van Ginneken et al., 2009). Several mechanisms have been proposed including (a) disruption of the reproduction and survival of offspring (Freese et al., 2017; van Ginneken et al., 2009; Larsson et al., 1991; van Ginneken et al., 2009), (b) reduction of lipid physiology and storage during growth (Belpaire et al., 2009; Byer, 2013; Cerón et al., 1996; Fernández-Vega et al., 1999; ICES, 2016b; Sancho et al., 1998), and (c) the reduction of male fertility (Bahamonde et al., 2013; Mills & Chichester, 2005). Several recent studies have begun to elucidate how eels are impacted by specific pollutants (Feunteun et al., 2014; Freese et al., 2017, 2019; Sühring et al., 2015), but we still do not clearly understand the effects, singly and cumulatively, of multiple and diverse pollutants. In consequence, the overall impacts of pollutants have mainly been hypothesized based on experimental knowledge of single pollutant exposure gathered from other fish species (Belpaire et al., 2016). This has led to an increased acceptance that contaminants could be a key factor in the decline of temperate eels on global scale (Belpaire et al., 2016; Freese et al., 2016). Determining the role of pollution in eel population dynamics and health is critically important, and quantifying to what extent, and at what level, contaminants affect reproductive success is crucial (Belpaire et al., 2019; ICES, 2013b, 2016b). This research may benefit from the technological progress of new methods such as the recent advances in artificial eel reproduction, genomic profiling tools and biomarkers, and telemetry. In particular, the artificial production of leptocephali of both *A. anguilla* (Butts et al., 2014) and *A. japonica* (Kagawa et al., 2005; Masuda et al., 2012; Okamura et al., 2014) will open new horizons for testing the effect of pollutants on eel reproduction.

3.2.4 | Is the viability of eel stocks affected by parasites?

Most studies on parasites and diseases of anguillid eels have involved *A. anguilla* (Conneely & McCarthy, 1986; Kennedy, 2007; Kirk, 2003). Parasite inventories compiled for other eel species mostly constitute snapshot studies on the diversity of their parasite assemblages (Hanek & Threlfall, 1970; Hine, 1978; Kennedy, 1995; Sasal et al., 2008), rather than analyses of biogeographical patterns or long-term surveys of parasite diversity. The catadromous, euryhaline, broad-niche, and migratory nature of eels means that they occupy many different types of river and coastal habitats and consequently have relatively higher parasite species richness than introduced fish which may occupy only a restricted niche (McCarthy et al., 2009).

Because of the diversity of parasites and the variation in composition of the species assemblages at infracommunity and component community levels, the effect of parasites on the condition factor of wild eels is poorly understood (Gérard et al., 2013). Several viral pathogens that cause increased mortality rates due to nonspecific haemorrhagic disease have been identified as being potentially threatening to *A. anguilla*—for example Eel virus European (EVE), Eel virus European X (EVEX) and Anguillid herpesvirus-1 (HVA) (McConville et al., 2018; Van Beurden et al., 2012).

The most comprehensive estimates of parasite effects on fitness have been of the invasive nematode *Anguillicola crassus* (Dracunculidae), which was first documented in the 1980s (Koops & Hartmann, 1989) in *A. anguilla* populations – the parasite was subsequently identified in *A. rostrata* (Barse et al., 2001). Use of molecular techniques has revealed that there is a relationship between expression of genes related to silvering processes and the presence of the nematode (Fazio et al., 2012; Schneebauer et al., 2017). Laboratory research indicates that infected eels show a more pronounced stress response when exposed to hypoxic conditions (Gollock et al., 2005), that infected silver eels may not be able to reach the spawning area due to the metabolic impacts of the parasite (Palstra et al., 2007), and physiological modelling suggests that the trans-oceanic migration would be significantly affected (Barry et al., 2014). Field evidence from silver eels migrating along the Swedish Baltic coast confirmed adverse effects on the swimming abilities and survival prospects of *A. crassus* infected eels (Sjöberg et al., 2009), although other studies have not come to the same conclusion (Simon et al., 2018). It seems certain that a chronic infection with this parasite alone, or associated with other impacts, will affect the ability of eels to migrate and reproduce effectively, but more work is needed on the impacts of *A. crassus* and how eels are adapting to infestation as it transitions from an acute to a chronic threat.

3.2.5 | Are present levels of exploitation sustainable for all life stages of eels?

While trends in catches have varied between countries, according to FAO statistics, internationally there has been an overall decline in legal landings in the last 30 years (FishStat Plus V.2.32, FAO; ICES, 2012a). Reporting of catches is inconsistent between countries, and where it is legally enforced, there are often discrepancies among records (Crook, 2014; ICES, 2016a; Shiraishi & Crook, 2015). Illegal, unreported, and unregulated (IUU) fisheries, and the associated trade, are poorly documented, if at all (Crook & Nakamura, 2013). Further, the uncertainties around IUU fishing and trade are of significant concern, as they undoubtedly mask a greater impact than that inferred from reported fisheries (Musing et al., 2018).

Glass, yellow and silver eels are fished using a wide variety of methods and effort. At the glass eel stage, several assessments of catchment-level exploitation in relation to recruitment indicate exploitation has been as low as 6% and greater than 95% depending on gear-type, presence of dams and location (Aranburu et al., 2015; Briand et al., 2003; Jessop, 2000; Tzeng, 1984) but the average exploitation rate, and the impact of fisheries on overall populations, remains poorly documented (e.g. Bornarel et al., 2018). Yellow and silver eel fisheries tend to be less economically valuable than glass eel fisheries (Knights, 2001), but these life stages are still widely exploited, and this is believed to impact subsequent recruitment (Åström & Dekker, 2007; Dekker, 2003a; Miller et al., 2009).

Globally, fishery regulations vary from permanent closures (e.g. Ontario Recovery Strategy, MacGregor et al., 2013) to setting quotas and limiting fishing seasons, gears and licences. In a number of countries, aboriginal fishing rights for eel exist and are separate to commercial quotas. In the case of *A. dieffenbachii*, the majority of these have been “shelved” to limit catch of this taonga—traditionally and culturally significant—species, such as the concern of the Māori people (Te Wai Māori Trust, pers. comm. 2019). In some cases, national regulations are absent despite international trade bans (Crook, 2014). Models developed that estimate recruitment at the continental and population levels may assist in setting and harmonizing sustainable exploitation rates (Bornarel et al., 2018; Drouineau et al., 2016). Synthesis of the available evidence on capture methods, handling and final destination of eels is also important in assessing the sustainability of exploitation. For example, the mortality rate of *A. anguilla* glass eels caught in trawl nets in France is relatively high compared to those fished with hand nets elsewhere (Briand et al., 2012; Josset et al., 2015), requiring larger catches to fulfil demand for live eels.

There remain many scientific challenges to defining and managing eel stocks at sustainable levels, especially as fisheries are not the only anthropogenic impact and exist in complex socioeconomic and environmental contexts. As such, it is important to improve data collection and catch reporting so as to design effective fishery management measures that take into account a wide range of factors and impacts at local, national and international levels.

3.3 | Theme 3: Management

3.3.1 | What stock assessment techniques are used for eels and how effective are they?

Ideally, any whole-stock assessment should be representative of the full spatial range and their accuracy and uncertainty considered (Jones, 2007). Recruitment is generally used as a primary data source/index of abundance for most species but because recruitment can occur across continental scales for anguillids, it is inevitable that the spatial range is subsampled and different data collection methods are used. Furthermore, recruitment is usually measured when eels enter freshwater, excluding the proportion of the population that stays in marine areas. Improving consistency and comparability is necessary, but standardizing to a single data collection method is difficult and many eel species are classed as data-poor.

Using *A. anguilla* as an example highlights the uncertainties involved in developing a stock assessment for any eel species because the diversity of impacts occurs across a large geographic range, and long intergeneration period creates a decadal time lag between action and effect on silver eel biomass (ICES, 2013b). The EC Regulation 1100/2007 (EU & Council of the European Union, 2007) requires EU Member States to assess eels in national waters, but because there is no clear stock–recruitment relationship to underpin the type of stock assessment typical for iteroparous commercial fish, the ICES Advice on *A. anguilla* stock (ICES, 2020) is based on recruitment trend indices from sentinel sites across the species range. The most recent statistical analysis of *A. anguilla* recruitment indices suggests that during the period 2011–2019, there has been an increasing trend, yet these are still below 10% of the baseline (1960–1979) (ICES, 2020) and the stock has yet to show signs of long-lasting recovery. EU Member States have also developed various methods to quantify silver eel biomass that may be empirical (i.e. through catching and/or counting) (Dekker, 2012; Rosell et al., 2005), or based on escapement models (e.g. Bevacqua et al., 2007; Briand et al., 2015; Defra, 2015; Oeberst & Fladung, 2012; Van De Wolfshaar et al., 2014; Walker et al., 2013). The feasibility of full stock assessments has also been investigated for *A. dieffenbachii* (Hoyle, 2016), *A. japonica* (Tanaka, 2014) and *A. rostrata* (Anon, 2017) but, as for *A. anguilla*, these have been significantly hampered by the difficulties in defining a stock–recruit relationship (ICES, 2013a).

Moving away from the "traditional" model for assessing stock size and developing assessment methods that account for a broad range of inputs and provide flexibility will enable greater consistency and application even when a population or species may be data-poor. In turn, this will allow regulators and managers to develop local and regional measures to protect and recover eel populations (Jacoby et al., 2015; Pohlmann et al., 2016) and ultimately reduce the uncertainty in stock assessments.

3.3.2 | How can we develop effective management frameworks for eel stocks at local, national and international levels?

Management strategies for eel species around the world are very diverse. Generally, the species that have historically been exploited have the most complex mechanisms of local, national and international management, although these vary in effectiveness. Arguably the most advanced management framework is the EC Regulation 1100/2007 (EU & Council of the European Union, 2007) that was imposed in 2007 to ensure all Member States with viable *A. anguilla* populations had developed Eel Management Plans (EMPs) to address declines. The flexibility provided by the regulation is helpful to manage at the regional, national and local level, however, it was stated in relation to EU EMPs "…post-evaluation of the 2012 Progress reports was hampered by the extensive variety of methods used to determine indicators, some of which were incomparable, and the confusing ways in which some data were reported. The standardization and coordination of the data collection, analysis and reporting should be made" (ICES, 2013a). This indicates that while standardization is not necessarily a feasible option for international management of any anguillid eel species, defining simple standards for data collection/analysis is important to enable assessments of the effectiveness of any management measures that are imposed. A recent review of the Regulation indicated that EMPs need to consider timescales of decades in the context of species recovery (European Commission, 2020).

It is also important to recognize that the EU EMPs do not cover the entire species range – although engagement of non-EU countries is increasing through the EIFAC/ICES/GFCM Working Group on Eel (ICES, 2016a) and regional initiatives such as the GFCM Mediterranean management plan (FAO, 2019). Further, the listing of *A. anguilla* in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) in 2014, offers a nonbinding framework for engagement with all range states.

The EU EMPs have gained a lot of attention, but there are other, more specific management mechanisms in place from the local to the international level. For example, the nonbinding "Joint Statement" relating to "International Cooperation for Conservation and Management of Japanese Eel Stock and Other Relevant Eel Species" was developed in 2014 by China, Japan, the Republic of Korea and Chinese Taipei with a focus on exploitation, aquaculture input of juveniles, and trade (Anon, 2014). However, there has been little detailed reporting on this agreement to date.

One consequence of tightening regulations on one species is that it may impact others. For example, *A. anguilla* was listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2009, and since 2010 there has been no legal export outside of the EU. This export ban has shifted pressure to other, non-CITES listed species, such as *A. rostrata* and *A. bicolor* (Musing et al., 2018), the latter of which is poorly understood, with little management in key export nations such as the Philippines (Crook, 2014).

It is important to note that anguillids are both revered and an important source of sustenance for Aboriginal peoples in North America, Australasia and Pacific islands, a longstanding association that has existed for centuries (Engler-Palma et al., 2013; Koster et al., 2020; Prosper & Paulette, 2002; Te Wai Māori Trust, pers. comm. 2019). As such, eel Aboriginal traditional knowledge provides important insights that can advance our understanding of the species and help address important information gaps. For example, recovery strategies for *A. rostrata* have shown the value of including these two types of knowledge (MacGregor et al., 2013).

From the short assessment of both general and threat-specific management initiatives above, it is clear that regardless of the scale, the development and application of an "end to end" approach to management frameworks is necessary. These include level of protection—including protected areas management (Cucherousset et al., 2007)—monitoring standards, data integration and reporting, species range, flexibility vs standardization, specificity of management framework, cultural and social elements, and regular effectiveness evaluation.

3.3.3 | What are the benefits and drawbacks of stocking eels?

The stocking of juvenile fish to compensate for aquatic habitat degradation and the decline or loss of natural recruitment is widespread. Because large-scale artificial reproduction of anguillid eels remains unviable (Masuda et al., 2012), stocking eels—and this may occur from glass eels through to yellow eels—is dependent on wild eels. Therefore, stocking does not provide a surplus to the stock but is based on the hypothesis that translocation from high-abundance areas may increase the survival of individuals in lower abundance areas.

At present, there is no evidence that stocked eels contribute to the spawning stock (ICES, 2011, 2016c) but it can increase silver eel escapement from river basins (Pratt & Threader, 2011; Wickström, 2001). Habitat, glass eel condition and density-dependent factors may impact stocking success (Dekker, 2015; Marohn et al., 2013; Simon & Dörner, 2014) and potential risks include altering local genetic structure (Als et al., 2011; Pavey et al., 2015; Pawson, 2012), introducing alien species (Marohn et al., 2014) diseases and parasites (Jakob et al., 2016; Kullmann et al., 2017; Pratt et al., 2019), and altering sex ratios and growth patterns (Côté et al., 2009; ICES, 2011). Several studies (without natural controls) demonstrate deviations from expected spawning migration patterns for stocked eels (Prigge et al., 2013; Sjöberg et al., 2017; Westin, 2003). Westerberg et al.,

(2014) showed that stocked and wild *A. anguilla* had similar migrating patterns, whereas Béguer-Pon et al., (2018) found that stocked *A. rostrata* escaped the Gulf of St. Lawrence at a significantly higher rate than wild eels. The broader impacts of eel stocking on freshwater ecosystems have not been studied.

To fully understand eel translocations, it is critical to be able to distinguish stocked eels from naturally immigrated ones. Several examples have been developed, based on destructive sampling methods (Kaifu et al., 2018; Pratt & Threader, 2011; Wickström & Sjöberg, 2014) and future development of nondestructive sampling will help considerably. However, alongside identification of stocked or natural eels, it is essential that methods are developed to ensure that the success of stocking practices is assessed (ICES, 2016c), enabling feedback into management plans.

3.3.4 | What role does aquaculture have to play in eel management?

Rearing and intensive growth methods for wild-caught juveniles to produce marketable yellow eels for human consumption are well established. However, production of artificially spawned and reared glass eels is still in the research and development stage (Okamura et al., 2014).

Significant progress in the artificial reproduction of eels has only been made for *A. japonica* (Kagawa et al., 2005; Masuda et al., 2012; Okamura et al., 2014). Corresponding efforts for artificial reproduction of *A. anguilla* (Butts et al., 2014; Marohn & Hanel, 2016; Tomkiewicz, 2012) and shortfin eel *A. australis* (Lokman & Young, 2000) have made some headway. The major bottleneck for any progress in rearing artificially produced larvae is the efficient provision of adequate feed (Ijiri et al., 2011). Tanaka et al., (2001) developed a leptocephalus diet which allowed *A. japonica* glass eels to be produced in captivity for the first time (Masuda et al., 2012; Tanaka et al., 2003) and some modifications have been proposed to improve this type of diet (Yamada et al., 2019). However, similar feeding trials in other anguillids have not yet been successful (Butts et al., 2016).

A closure of the reproductive cycle of anguillid species other than *A. japonica* and further advances in a mass production of glass eels could relieve pressure on natural populations worldwide by reducing, or removing, the demand for wild aquaculture seed. However, the scale of producible glass eels—for example thousands per year in an institute—compared with the aquaculture demand of wild juveniles—at least a 100 million per year—is significantly lacking. Research into increasing the proportion of artificially cultured eels that survive into the glass eel stage is critical to scaling up commercial aquaculture methods.

3.3.5 | What is the impact of trade in eels?

Despite declines in recruitment and increasingly strict regulations, many anguillid species are harvested, farmed, traded and consumed on a global scale (Shiraishi & Crook, 2015). East Asian countries have historically had the highest eel consumption rates—primarily Japan. But in recent years, a proportion of Japan's consumption has been replaced by demand in mainland China, South Korea and other smaller markets outside the region (Shiraishi & Crook, 2015) with the growth in popularity of Japanese cuisine worldwide. Over 90% of all *Anguilla* production is dependent on growing out wild-caught juvenile eels (FAO, 2017) with only a small proportion being harvested at yellow and silver stages for direct consumption. Historically, farming and trade in East Asia involved *A. japonica*, but due to reduced availability of this species during the 1990s, large quantities of *A. anguilla* glass eels were imported for farming (Ringuet et al., 2002). Concerns regarding the impact of international trade on *A. anguilla* led to it being listed in CITES Appendix II in 2009 and in December 2010, the EU ceased trade outside of member countries. Since the early 2010s, the Americas and Southeast Asia became increasingly important sources of juvenile eels for farms in East Asia (Crook, 2014; Crook & Nakamura, 2013; Musing et al., 2018). Some of these newer fisheries have emerged in areas where the scale of exploitation has been unmonitored and/or unreported and the impact of a sudden increase in exploitation on these species is not understood (Gollock et al., 2018).

While growing awareness and strengthened enforcement has led to seizures of juvenile *A. anguilla*, illegal trade remains an issue (ICES, 2016a; Musing et al., 2018; UNODC, 2016). The demand for *A. anguilla* remains high in China; with 20 tonnes of juvenile *A. anguilla* reported to be supplied to eel farms in the 2015 eel year alone (Fan, 2016; according to Shiraishi and Crook (2015), an "eel year" begins in September. The 2015 eel year means the year starting in September 2014 and ending in August 2015), not all of which may have been traded legally. Illegal fishing and trade are prevalent for other eel species with instances of IUU activity having been identified in *A. japonica*, *A. rostrata* and *A. bicolor* (Crook, 2014; Fisheries Agency of Japan, 2017; Weiner, 2017). Other concerns include false declarations of species because glass eels of different species are extremely difficult to distinguish from one another morphologically. Monitoring and enforcement of fisheries and trade need to be strengthened to ensure that eels and eel products exported for grow-out and/or consumption are both sustainable and legal (Gollock et al., 2018; Musing et al., 2018).

4 | CONCLUSIONS: WHAT DOES SUCCESS LOOK LIKE?

The complexity of anguillid eel life histories, coupled with their wide geographic distribution presents a formidable challenge for prioritizing management. The progress in science, conservation and management of anguillid eels in recent years is considerable, however, the stock status of many remains of great concern, particularly for northern temperate species. Clearly, the long-term goal of management efforts is to reduce human impacts, primarily in the growth habitat, but a number of problems remain regarding the implementation, assessment and effectiveness of management measures as biology and ecology, particularly for tropical species, remains poorly understood. In reality, making accurate estimates or measures of recruitment, population size and escapement is extremely challenging, and multiple methods are used across and within species. Due to the large inconsistencies and gaps in data collection and reporting, it is difficult to draw robust or general conclusions about the effectiveness of the management measures being implemented (Bevacqua et al., 2015; Jacoby et al., 2015). This has led to a focus on whether actions have been implemented (e.g. closing of a fishery), rather than whether the measures are successful (e.g. increase in escapement) (Schiavina et al., 2015). These localized management and conservation efforts are to be encouraged, but without improved engagement at the national and international level, the situation is unlikely to measurably improve due to the complex life history of eels (Jacoby et al., 2015). Harmonization of data collection, reporting and analysis through the use of minimum basic standards would allow for more robust comparisons, both within and between, years, range states and species. This approach would also improve collaboration and coordination, something that while obviously challenging, is essential when working with panmictic species that can also exhibit continental transboundary migrations.

Nonetheless, international efforts to improve and better coordinate eel management have been made over the last two decades. Some regions have drafted official management plans, such as the Interstate Fishery Management Plan for *A. rostrata*, created by the Atlantic States Marine Fisheries Commission (ASMFC, 2000, 2013, 2014, 2017) and the EMPs (EU, 2007; ICES, 2013b). The Association of Southeast Asian Nations (ASEAN) member states have, since 2015, established management initiatives for anguillid eels, which includes developing policy and research (SEAFDEC, 2018) and efforts have also been made towards coordinating management for *A. japonica* between China, Chinese Taipei, Japan and the Republic of Korea (Anon, 2014). Typically, such plans emphasize several management measures, which may include controlling predators, creating and maintaining access to growth habitats, regulating eel fisheries and reducing other sources of anthropogenic mortality. Increasingly, the importance of adaptability of management is becoming clear.

Ultimately, there remains a question on what “success” and/or “recovery” looks like in real terms. Improving data collection and continuing to evolve management and conservation frameworks will be key to ensuring the sustainability of anguillid eel populations into the future. The IUCN has recently begun developing “The Green List of Species” in order to examine the effectiveness of conservation initiatives, and it is possible that, although it is a generic framework for assessing any species, it will prove to be a useful mechanism to be used by stakeholders in concert with the Red List (Akçakaya et al., 2018). Ultimately, defining long-term targets for population size and status will be necessary so as to

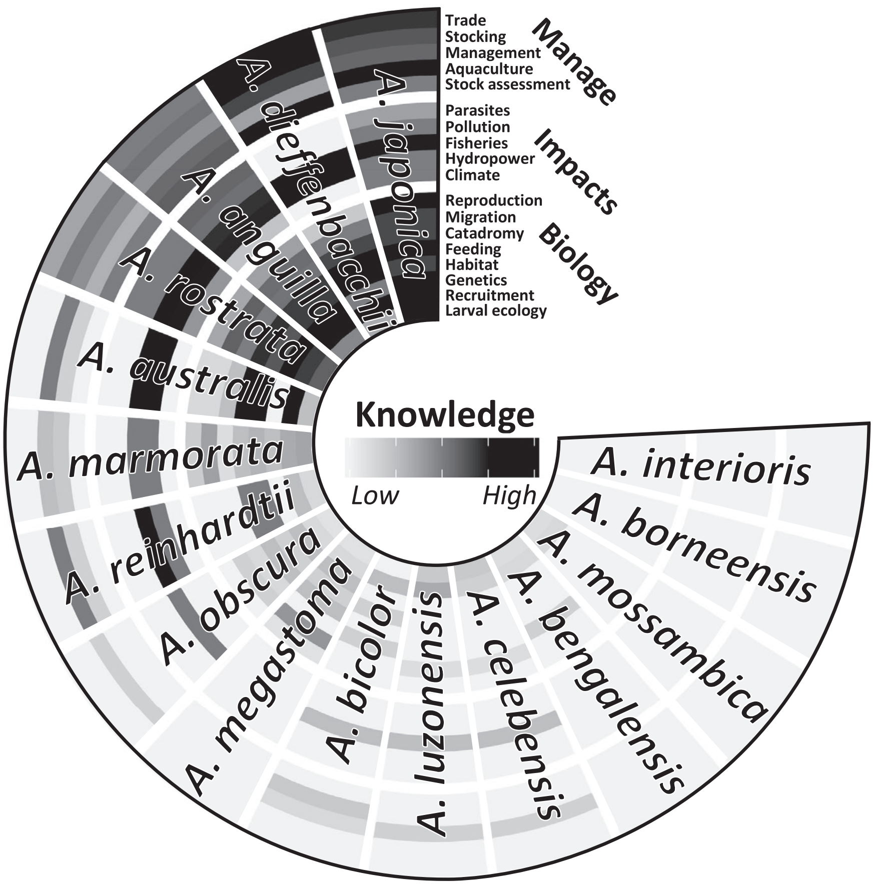

FIGURE 2 Knowledge mapping exercise. Shading corresponds to high (intense) or low (pale) knowledge. Rings correspond to topics listed alongside each ring at the top of the figure, which are grouped into three overarching themes. The order of species shows the ranking of average knowledge score (*Anguilla japonica* is highest)

maximize the benefit of our increasing knowledge and understanding of anguillid eels around the world.

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CONFLICTS OF INTEREST

None.

AUTHOR CONTRIBUTIONS

All listed authors fulfil the Authorship policy criteria of Fish & Fisheries.

DATA AVAILABILITY STATEMENT

Data sharing is only applicable to this article with respect to the expert assessment of eel knowledge presented in Figure 2. These data are available from the corresponding author upon reasonable request.

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