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Synergistic patterns of threat and the challenges facing global anguillid eel conservation

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HIGHLIGHTS

- The first global review of anguillid population data and conservation status.
- Eel population data currently fall short of required length and geographic range.
- Multiple, synergistic, yet variable threats face eels across all life-history stages.
- Key recommendations made for input into international eel conservation strategies.

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ABSTRACT

With broad distributions, diadromous fishes can be exposed to multiple threats at different stages of development. For the primarily catadromous eels of the family Anguillidae, there is growing international concern for the population abundance and escapement trends of some of these species and yet incomplete knowledge of their remarkable life-histories hampers management and conservation. Anguillids experience a suite of pressures that include habitat loss/modification, migration barriers, pollution, parasitism, exploitation, and

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fluctuating oceanic conditions that likely have synergistic and regionally variable impacts, even within species. In beginning to redress this rather fragmented picture, we evaluated the extinction risk of these species using the IUCN Red List of Threatened Species Categories and Criteria to infer population-wide trends from catch and monitoring data. Here we consolidate and build upon these species assessments by presenting an overview of the current state of global eel data and conservation, categorising the knowledge gaps and geographic regions where resources are needed and discussing future recommendations to improve our understanding of anguillids. We find stark disparity between the quality and length of data available to assess population trends and conservation priorities in temperate and tropical anguillids. Of the 13 species assessed, four were listed as 'Threatened' (Vulnerable, Endangered or Critically Endangered); four were Near Threatened, three were Data Deficient and two were deemed Least Concern. Comparing with other diadromous species, we examine the multiple threats that impact eels during their different life-history stages, highlighting the challenges of applying the Red List Categories and Criteria to geographically-expansive, catadromous and panmictic groups of species.

1. Introduction

The reduction in both quality and quantity of freshwater, estuarine and coastal habitat and the resulting loss of biodiversity have become a cause for global concern (Dudgeon et al., 2006; Lotze et al., 2006 and Davidson, 2014). The need to increase monitoring efforts and co-ordinate international conservation strategies for freshwater fish populations has never been greater, particularly for the relatively small number of diadromous fishes that migrate between saline and freshwater environments (McDowall, 1999; Jelks et al., 2008; Limburg and Waldman, 2009). However, achieving these goals for species that have complex life-histories and broad geographic ranges can often be difficult, especially as a disproportionate percentage of the diadromous fishes are also heavily exploited (McDowall, 1992).

As a taxonomic group, freshwater eels of the family Anguillidae are globally distributed, inhabiting the fresh waters, brackish estuaries and coastal waters of more than 150 different countries (IUCN, 2014). Despite its frequent use, the term 'freshwater' eel can be misleading. Anguillid eels are generally facultatively catadromous, as it is known that a proportion of any population may reside in estuaries, lagoons and coastal waters, rarely, if ever, entering fresh water (e.g. Arai et al., 2004 and Lamson et al., 2006). Their life-history is further complicated by multiple life stages, semelpary, and panmixia—their pelagic spawning areas are far from their growth habitats[1] (Aida et al., 2003; van Ginneken and Maes, 2005).

Like many other fish species, anguillid eel populations, most notably in temperate Northern Hemisphere regions, have seen dramatic declines in recent decades because of a number of factors, including overexploitation (Haro et al., 2000; Dekker, 2003; Casselman, 2003; Tsukamoto et al., 2003; Miller and Casselman, 2014). Indeed other diadromous species have suffered a similar fate with all major sturgeon fisheries having now past their peak productivity levels (Pikitch et al., 2005) and many salmonids showing declines in abundance and distribution throughout historically productive habitats (Thurow et al., 1997). However, it would be misleading to claim that declines in anguillid eels are solely due to exploitation as it is increasingly apparent that these are driven by multiple factors. Barriers in the form of dams and weirs, which prevent the upstream and downstream migration of eels and reduce available freshwater habitat or, worse still, cause the direct mortality of migrating eels, are a major concern (Jansen et al., 2007). For example, two large hydropower facilities in the St. Lawrence River, Canada were estimated to cause cumulative annual downstream silver eel mortality of ∼40% (Verreault and Dumont, 2003) and across the waterways of Europe over 24,000 hydropower plants are now installed (van der Meer, 2012). The role of changing oceanic conditions as a result of climate change is increasingly being discussed in relation to eel larval migration and the subsequent recruitment of glass eels to continental waters (Castonguay et al., 1994; Dekker, 2004; Bonhommeau et al., 2008; Miller et al., 2009; Baltazar-Soares et al., 2014; Pacariz et al., 2014) although decoupling the impact of climate change from historic, natural variability in recruitment is difficult (Kim et al., 2004). Other factors that are implicated in affecting anguillid abundance include disease and parasites, predation, and pollutants (Robinet and Feunteun, 2002; Fazio et al., 2012; Wahlberg et al., 2014). As such, the conservation of anguillid eels faces a myriad of scientific, political, socioeconomic and logistical challenges that require broad and co-ordinated input from a variety of national and international stakeholders. These challenges mean that, currently, a lack of integrated governance of eel remains a significant obstacle in many parts of the world.

While the conservation and management of anguillid eels is, to a large degree, hampered by the fact that there are still huge knowledge gaps relating to these species, it is important that this dearth of knowledge does not impede action (Darwall et al., 2009; IUCN, 2012a,b). Amid growing concern among stakeholders relating to the decline of a number of anguillid

[1] The giant mottled eel, *Anguilla marmorata* is believed to have more than one spawning location and therefore may not be truly panmictic (Minegishi et al., 2008).

species, the International Union for Conservation of Nature Species Survival Commission (IUCN SSC) Anguillid Specialist Sub-Group (ASSG) was established in 2012 under the IUCN Freshwater Fish Specialist Group (FFSG). The IUCN Red List of Threatened Species is widely regarded as one of the most comprehensive and scientifically rigorous global standards by which to categorise and compare the relative threat of extinction of plant and animal species. To date, the Red List contains 76,199 assessed species (IUCN, 2014), many of which are not threatened. Inclusion of the anguillids on the Red List provides an important repository summarising current information on distribution, abundance, ecology, conservation and possible threats for each species. Because of their typically broad, international distribution and complex, catadromous life histories, monitoring of anguillid eel population dynamics through time and across their geographic ranges is challenging, often resulting in sparse, patchy or imbalanced data. As such, the application of the IUCN Red List Categories and Criteria (IUCN, 2012a,b) to the anguillids came with a unique set of challenges that we feel require formalising to help inform future conservation actions. Here we go beyond the assessments, that present species-specific details, and review the quality of data available globally for calculating anguillid population trends, highlight the knowledge and data gaps that require attention to improve conservation, and consolidate and review information on the major threats facing eels drawing parallels with other diadromous species assessments. We discuss how we approached the challenges of applying the Categories and Criteria to eels and offer recommendations for anguillid conservation going forward.

2. Methods

The methods described here represent the data categorisation, filtering and analysis that took place during the Red List assessments and the meta-analyses conducted on the assessment output. According to the most up-to-date phylogeny (Teng et al., 2009) there are 16 species of anguillid eel, three of which have been proposed by some researchers as having two sub-species each (*Anguilla australis*, *Anguilla bengalensis* and *Anguilla bicolor*). Species-specific data describing the distribution, population trends, ecology and habitat type, use and trade, threats and conservation, where available, were collated from as complete a geographic range as possible for each species.

In accordance with IUCN Red List protocol, a relative threat of extinction is determined on a categorical scale (Fig. 1) ranging from Least Concern (LC) and Near Threatened (NT), through three 'Threatened' categories of increasing severity, Vulnerable (VU), Endangered (EN) and Critically Endangered (CR). These are determined by a set of criteria aimed at detecting risk across a variety of organisms and life histories, which for the eels, relate to a reduction in population size or geographic range. Two final categories report those species which are thought to be Extinct in the wild (EW) and Extinct (EX). Full details of the Red List Categories and Criteria can be found at the following link (http://www.iucnredlist.org/technical-documents/categories-and-criteria). Species found to be NT are either nearing a threat category threshold or are likely to meet a threshold in the near future without the intervention of conservation efforts. In addition, species can be deemed Data Deficient (DD) should insufficient data be available to identify the species risk of extinction (IUCN, 2012b, Fig. 1).

2.1. Data analysis

Because of their broad geographic range and the potential for relatively large populations, anguillid eel species were evaluated predominantly under *Criteria A*[2] that quantifies extinction risk based on a reduction in population size over a period of 10 years or three generations, whichever proves longer. It should be noted that in relation to anguillids, 'population' specifically refers to abundance of the continental phase (yellow eels) while recruitment relates to arriving glass eels/elvers, and escapement to departing silver eels. Available metrics for the separate life-stages were examined individually but ultimately pooled in order to apply the Red List criteria. While escapement is the nearest proxy for a spawning stock, there are few data sets that accurately estimate this for any species and as such changes in recruitment and population metrics and what affect their declines might have on escapement, were considered in pooling the data. As defined by IUCN, generation length is intended to reflect the turnover rate of breeding individuals in the population (IUCN, 2012b) and in semelparous species like freshwater eels that breed only once, the generation length will equal the average life span. For all anguillid species, however, latitudinal variation and sexual dimorphism significantly affects average generation length because of differences in temperature, distance from spawning ground to maturing habitat and other biological and environmental influences (Holmgren et al., 1997; Feunteun et al., 2003; Cairns et al., 2009; Daverat et al., 2012, see also Table 1). The American eel (*Anguilla rostrata*), for example, has a broad range of generation lengths across its vast distribution from a mean (range) of 17.5 yrs (5–43) in the St Lawrence River system, Canada, to 5.6 yrs (1–16) across the Southern Atlantic coastal states of South Carolina, Georgia, Florida, Louisiana and Texas (Casselman, 2003). In order to estimate generation times population data, if available for a species, were sub-divided into regions and where possible spawner age was determined, adjusting for oceanic duration, spawning, and associated emigration time, as well as leptocephalus and glass eel recruitment time, to determine generation time by region. This was then weighted according to the estimated percentage of the population in each region, to provide a mean generation time for the species. For many of the tropical species where ecological studies have yet to be carried out, generation estimates were inferred from expert opinion and

[2] Other criteria (B to E) relate to a reduction in geographic range, low numbers of mature individuals or a very low number of localities in which the species is found. Under Category A, a 'threatened' status is determined by the % population decline over three generation lengths where the cause has not ceased: VU = 30%–49%; EN = 50%–79%; CR = 80%–99%.

comparison with analogous species and localities. While such estimates are not perfect, future assessments will be able to incorporate up to date data to improve them.

To explore the current state of anguillid population data globally, species data sets were ranked on a categorical, linear scale in order to prioritise those most suitable for assessing population change using the Red List Categories and Criteria. The simplified scale ranged from effort-based metrics of silver eel spawning and escapement as the best proxy for the spawning stock, to non-effort landings data for glass eel recruitment and trade data (see Table A1 for details on the full data ranking). Where catch per unit effort (CPUE) and fisheries independent monitoring (FIM) data were rare (e.g. for most tropical species), glass eel landings data were used as a proxy for recruitment. We acknowledge the potential ambiguity of assigning a linear scale to the circular life history of anguillids, however, for illustrative purposes (see Fig. 2), we feel this classification provided a suitable summary.

The IUCN Criterion A calculator was used as a guide to inform expert opinion on the qualitative components of the assessments. The Criterion A calculator is designed to identify declines, at constant exponential rates, in the different sub-populations, and to estimate the current population levels and relative percentage change over three generations. As population-wide data were incomplete for all species, this quantitative method was used not for automatically identifying the rate of population change or directly assigning a category, but only for guiding the discussion to identify the final category. All accumulated species-specific data contributed to the global analyses in this paper, namely the geographic distribution of Red List categories, quality, quantity, spread and gaps in population data. Additionally, to help gauge the relative global conservation status of anguillids, data on threats facing other diadromous genera, namely sturgeon and salmonids, were summarised directly from their respective IUCN Red List web pages (IUCN, 2014) for comparison.

3. Results

Application of the Red List Categories and Criteria revealed that four species of anguillid eel were classified as threatened due to an estimated decline in breeding stock (VU, EN × 2 and CR), four were NT and two were considered LC, underlining concern for this taxonomic group as a whole. For the remaining three, data were extremely sparse and these species were deemed DD and therefore urgently require study. Of the four previously assessed species, one remained LC, two have been up-listed from LC to NT and one, *Anguilla anguilla* (European eel), remained CR. Despite the continuation of the CR listing, it was felt that the situation could be improving for the European eel because of the development of national management plans in European Union range states in addition to recent small increases in recruitment indices. A summary of the outcome of this current assessment of the anguillid eels and the criteria met is given in Table 1. At the time of writing, the remaining three species are currently being assessed for an Australasian project.

Substantially more CPUE and FIM data were available for the primarily temperate versus exclusively tropical eel species. Focusing on the three most studied temperate anguillids, data set quality and length, on average, fell short of their respective three generation length time frame (Fig. 2). Consequently, this forces us to use extrapolations and inferences to predict temporal trends in populations of different life-history stages, which although not ideal, is the only option currently available. Fig. 2 is a simplified illustration of the variation in data between species; however, as discussed below, the importance of continental recruitment and older stage eel metrics might vary between species in different region due to topography of the coastline. Such geographic differences likely reflect multiple issues including the differential historic exploitation of eels between regions (i.e. longer fisheries records); differences in the economic capacity of developed and developing countries to establish surveys and monitoring schemes; and variation in national conservation and management priorities.

Three of the four threatened species are the most commercially important species of the genus *Anguilla*—the European eel, *A. anguilla* (CR), the Japanese eel, *A. japonica* (EN) and the American eel, *A. rostrata* (EN). For *A. anguilla*, for example, data were of the longest and highest quality of all species (Fig. 2). Silver eel data, however, were scarce but informative, and while this was not geographically representative of the stock as a whole (ICES WGEEL, 2013), these data indicated a mean decline in silver eel escapement numbers of 50%–60% over the period of three generations (45 years). The data that related to *A. anguilla* yellow eels suggested that over the same time period there had been a slightly greater decline compared to silver eels. Compounding these declines in escapement of maturing eels and populations of yellow eels, there had been substantial declines (90%–95%) in recruitment of the glass eel phase of *A. anguilla* across wide areas of its geographic range, a result that supports the analysis that has been published by the International Council for the Exploration of the Sea (ICES) in their most recent annual report (ICES WGEEL, 2014). These data, in conjunction with assessments of past, present and future threats, and associated management measures, determined that this species should remain CR.

The available data for glass, yellow and silver eels for *A. japonica* indicated that this species had declined in abundance across its range over the last 30 years (ca. three generation lengths). This species was thus assessed as EN due to an estimated reduction in the spawning population of approximately 50% during this time period, a result consistent with classification by the Japanese Environment Ministry.[3] FIM data for eels in East Asia is particularly sparse and consequently the discussion surrounding the assessment relied predominantly on fisheries catch data with some standardised CPUE from parts of its

[3] http://www.japantimes.co.jp/life/2013/02/02/environment/ministry-officially-classifies-japanese-eel-as-species-at-risk-of-extinction/#.VUntXPm6flU

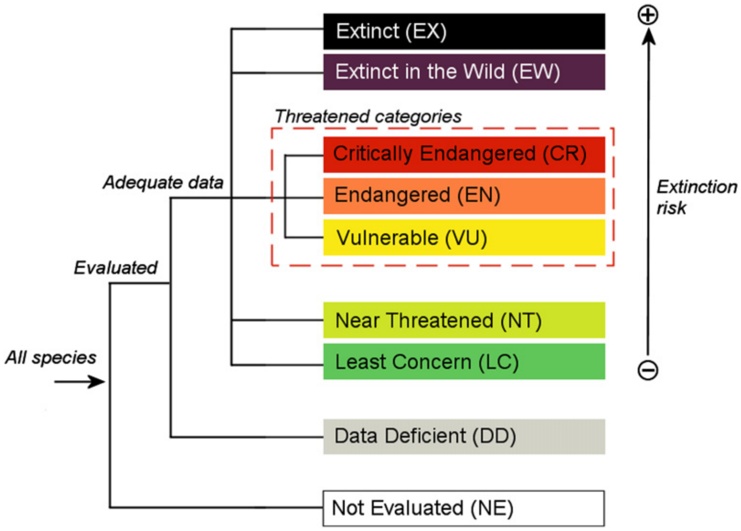

Fig. 1. Summary of the IUCN Red List categories (IUCN, 2012a,b) (1 column).

Table 1
Summary table of the global Red List status of species of freshwater eel assessed in 2013 by the IUCN Anguillid Specialist Sub Group (ASSG). The anguillids that are found in New Zealand – *Anguilla australis*, *Anguilla dieffenbachii* and *Anguilla reinhardtii* – are being assessed as part of a regional project and as such are not considered here.

Species	English common name	Generation length[b] (yrs) (*period of assessment*)	Region	IUCN Red List status (*previous assessment*)
Anguilla anguilla	European eel	15 (*45*)	Temperate	**CR**-A2bd + 4bd (*CR*)
Anguilla bengalensis[a]	Indian/African mottled eel	12 (*36*)	Tropical	**NT**(*LC*)
Anguilla bicolor[a]	Indonesian/Indian shortfin eel	6 (*18*)	Tropical	**NT**-*nearing* A4d (*LC*)
Anguilla borneensis	Indonesian longfinned eel	6 (*18*)	Tropical	**VU**-A2c
Anguilla celebesensis	Celebes longfin eel	8 (*24*)	Tropical	**NT**-*nearing* A4d
Anguilla interioris	Highlands longfinned eel	8 (*24*)	Tropical	**DD**
Anguilla japonica	Japanese eel	10 (*30*)	Temperate	**EN**-A2bc
Anguilla luzonensis	Philippine mottled eel	8 (*24*)	Tropical	**NT**-*nearing* A4cde
Anguilla marmorata	Giant mottled eel	12 (*36*)	Tropical	**LC** (*LC*)
Anguilla megastoma	Polynesian longfinned eel	10 (*30*)	Tropical	**DD**
Anguilla mossambica	African longfin eel	10 (*30*)	Tropical	**LC**
Anguilla obscura	Pacific shortfinned eel	6 (*18*)	Tropical	**DD**
Anguilla rostrata	American eel	12 (*36*)	Temperate	**EN**-A2bd
Anguilla australis[a]	Australian/New Zealand shortfin eel		Temperate	*Not Assessed*
Anguilla dieffenbachii	New Zealand Longfin eel		Temperate	*Not Assessed*
Anguilla reinhardtii	Speckled longfin eel		Temperate	*Not Assessed*

[a] Species that have historically been split into two *subspecies* divided by geographic region.
[b] See *Data analysis* for details of how generation lengths were calculated.

range (e.g. Japan), where data were relatively more abundant. Improvements in the ranked data quality of this species will be essential for future accurate assessments of this species (Fig. 2).

Long-term FIM and CPUE data were available for *A. rostrata* from the St. Lawrence River system to the Caribbean Gulf of Mexico and the Mississippi River system, although data from this southern portion of the distribution were sparse (see recent review by Benchetrit and McCleave, 2015). The majority of data for the American eel related to young yellow eels although the few data sets available for glass eel recruitment and silver eel escapement suggested a population decline of ∼50% over three generations (36 years) and a slightly greater decline (50%–60%) in yellow eel abundance, placing *A. rostrata* in the EN category.

Growing concern for many of the tropical anguillid species, particularly those inhabiting parts of the Western Central Pacific, was reflected in the assessments of species within this area. *A. borneensis*, has a range restricted almost exclusively to Borneo and parts of Sulawesi, Indonesia. Assessed as VU, this species appears to have been extirpated in the Karabakan River, where in the 1960s it was once abundant across multiple sites (Inger and Kong, 1962; Tsukamoto and Aoyama, 2014, pers. comm.).Significant deforestation along the river edge is thought to have been the main cause for this reduction in population and range, although, as with all anguillids, the stressors are likely to be synergistic and/or cumulative.

Shifting exploitation has already impacted *A. rostrata*; reported imports of 'live eel fry' into East Asia from the Americas have increased three fold over the last five years (peaking at 44 t in 2013) as a result of both reduced recruitment of

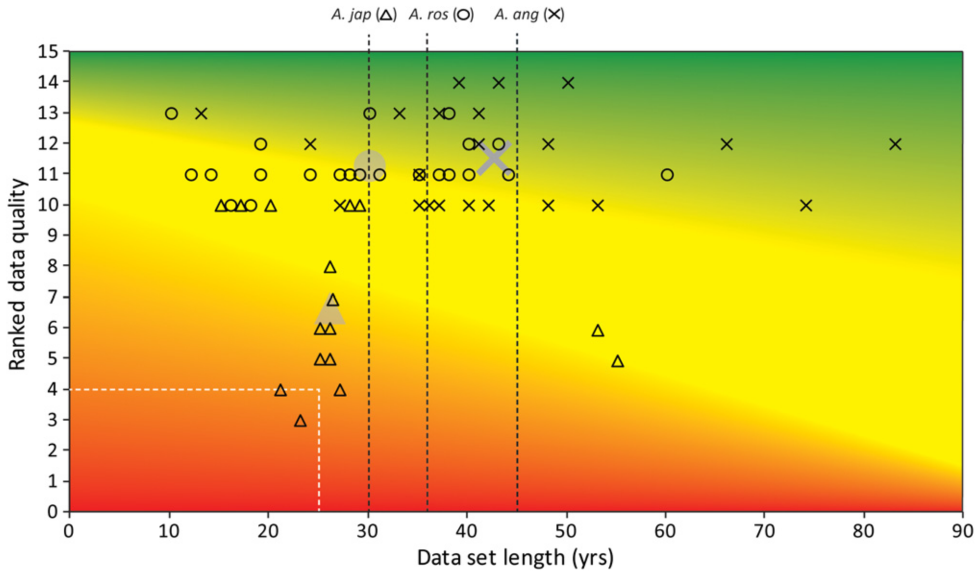

Fig. 2. Longevity and ranked data quality for the three most comprehensively studied, northern temperate species data sets based on their desirability in applying the Red List Categories and Criteria (green being most preferred). Each point refers to a single data set for a species (larger grey points represent species means). Black dotted lines show three generation lengths for *A. anguilla* (cross), *A. japonica* (open triangle) and *A. rostrata* (open circle). White dotted area represents where all available data on tropical species lie. See SI Table 1 for data quality ranking (1.5 columns). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the Japanese eel and the closure of the European eel export market (Crook and Nakamura, 2013; Shiraishi and Crook, 2015). There are now signs that several tropical species are also becoming increasingly targeted as replacements for eel culture. For example, in 2011–2013, there was a sharp increase in glass eel exports from the Philippines, a range state of the Indonesian/Indian shortfin eel (*A. bicolor*), as this species meets the high demand for 'plain' coloured eels that was once filled by *A. japonica* and *A. anguilla* (Crook, 2014). Consequently, *A. bicolor* has been up-listed to NT from its previous listing of LC in 2010. The recently described Philippine mottled eel, *A. luzonensis*, has a highly restricted geographic range, predominantly two localities in the Cagayan river system on the island of Luzon (Watanabe et al., 2009) and was listed as NT based on a suspected future population decline under current threats which mean it was close to meeting the criteria for VU. Without genetic analysis, however, this species is almost impossible to distinguish, at least in the juvenile phase, from other anguillid eels from the same region (*A. celebesensis* and *A. interioris*) suggesting that *A. luzonensis* should be prioritised for reassessment when the taxonomic/geographic uncertainty has been resolved, in order to determine its true distribution (Aoyama et al., 2015). In the Indian Ocean, *A. bengalensis*, has been up-listed to NT from LC due to a decline in its range and regional abundance (Freyhof, 2014, pers. comm.). Equally, in the Central and South Pacific Ocean where data are very sparse, eel species which may include *A. obscura* (DD) and *A. megastoma* (DD) are increasingly being targeted for export to culture facilities in China (Sasal, 2014, pers. comm.). The giant mottled eel, *A. marmorata* and the African longfin eel, *A. mossambica* were the only species listed as LC, however this does not preclude the need to increase monitoring efforts for these species in many of the remote localities in which they are found. While global Red List assessments call for organisms to be assessed at the species level, several of the anguillids (*A. bicolor*, *A. bengalensis* and *A. marmorata*) would arguably benefit from regional assessments to aid the stock management of distinct sub-populations. The geographic distribution of Red List classifications is provided in Fig. 3.

3.1. Synergistic threats to anguillid populations

Throughout their global distribution it was apparent that anguillids face a broad and dynamic range of threats. Further, our ability to determine the individual effects of these threats on population trends is complicated by the multiple life-stages across a range of environments, facultative catadromy and panmixia that characterise this genus. At any one stage of the eel life cycle, individuals are potentially exposed to multiple threats (Fig. 4). The impact of these threats, either individually or synergistically, appeared very regional and life-stage specific. Consequently, how these stressors combine to contribute to declines in abundance of particular life-stages is still poorly understood and as such the Red List assessments should be seen as an initial platform with which to formalise and highlight these threats as areas that require considerable attention to support strategic conservation.

Of the 11 overarching IUCN coded threats which relate to human activities or processes impacting species, all of the 13 species were deemed potentially threatened by *Biological resource use*, which includes the fishing and harvesting of the species for intentional use (Fig. 5). Anguillid species are commercially important in a number of countries and the

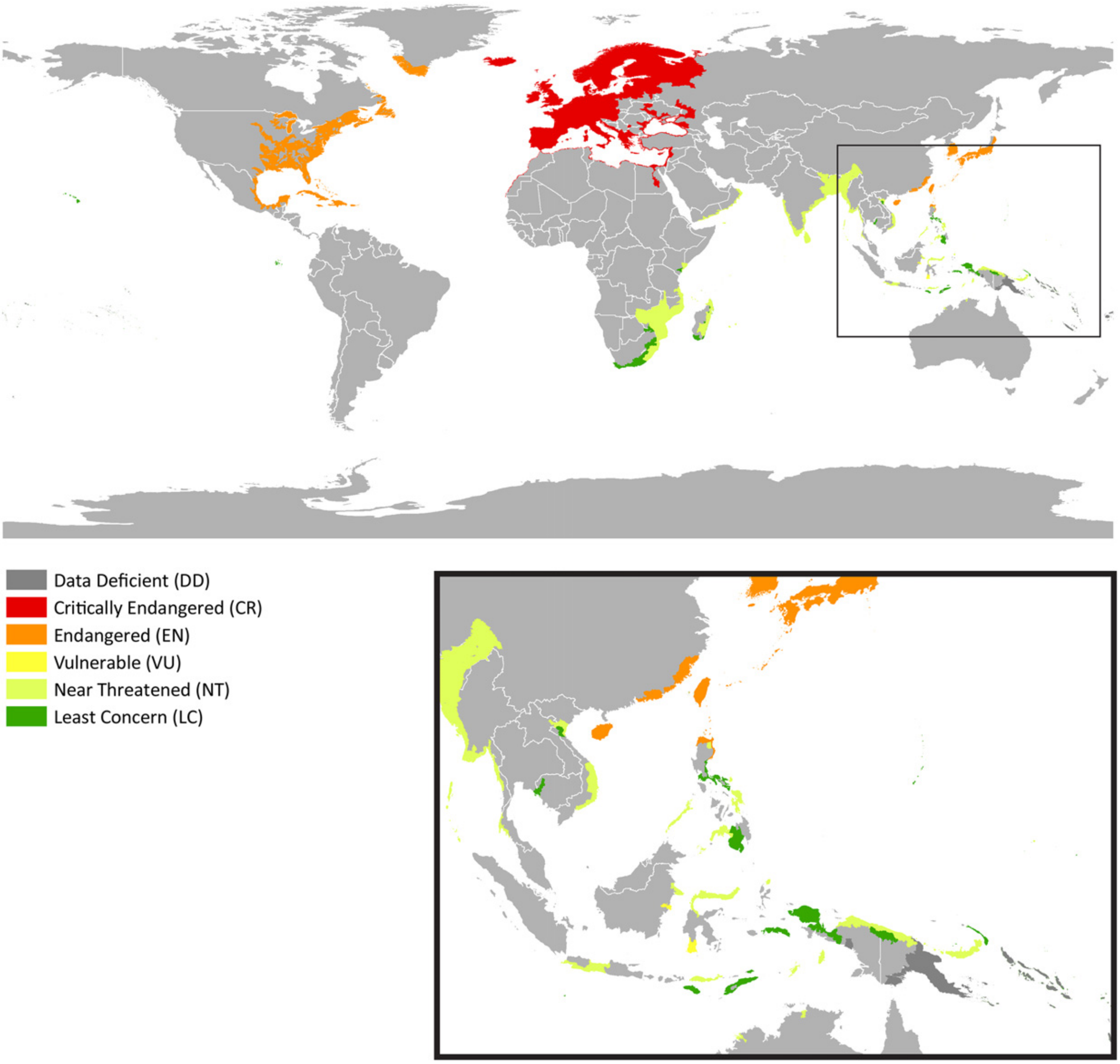

Fig. 3. Global coastal and freshwater native distribution (150 countries) of the assessed anguillid eels coloured by Red List classification (inset: East Asia/South Pacific). Marine migration paths and breeding locations have not been included because of their complexity and uncertainty in many species. Note the large areas of Papua New Guinea and many islands of the South Pacific Ocean that require baseline monitoring of anguillid population dynamics and recruitment in order to assess their population status (2 columns).

exploitation of the glass eel stage for culture facilities is ongoing (Crook and Nakamura, 2013). Equally, however, all species were also found to be potentially impacted by *Climate change*, which in relation to the anguillid eels was identified as changes to oceanographic factors such as current systems, primary production and thermal regimes. Another major threat which was thought to affect 85% of anguillid species was *Natural system modifications*, a broad descriptor that encompasses the abstraction of water and the installation of dams and other water management systems. Despite the ability of eels to climb moist surfaces, large dams can restrict juvenile upstream movements, impacting localised population densities (Hitt et al., 2012) and thus sex ratio and reproductive output from specific localities (McCleave, 2001). In addition, they can also prevent adult escapement of silver eels to the ocean and cause direct mortality of silver eels passing through hydropower turbines as they emigrate to their spawning grounds (ICES 2002; Jansen et al., 2007 and MacGregor et al., 2009).

In addition to these stressors, eels were also found to be broadly impacted by pollutants, particularly from energy production and mining activities (Robinet and Feunteun, 2002) and also by disease and parasites. The introduced parasitic nematode *Anguillicola crassus* is thought to cause swimbladder damage and have metabolic impacts impairing the ability of European and American eel to migrate back to the spawning area (Vettier et al., 2003; Gollock et al., 2005; Palstra et al., 2007; Sjöberg et al., 2009; Fazio et al., 2012). Human-induced increases in natural predators, such as cormorants, are also cited as playing a role in the population dynamics of some species (Carpentier et al., 2009) in addition to suspected oceanic

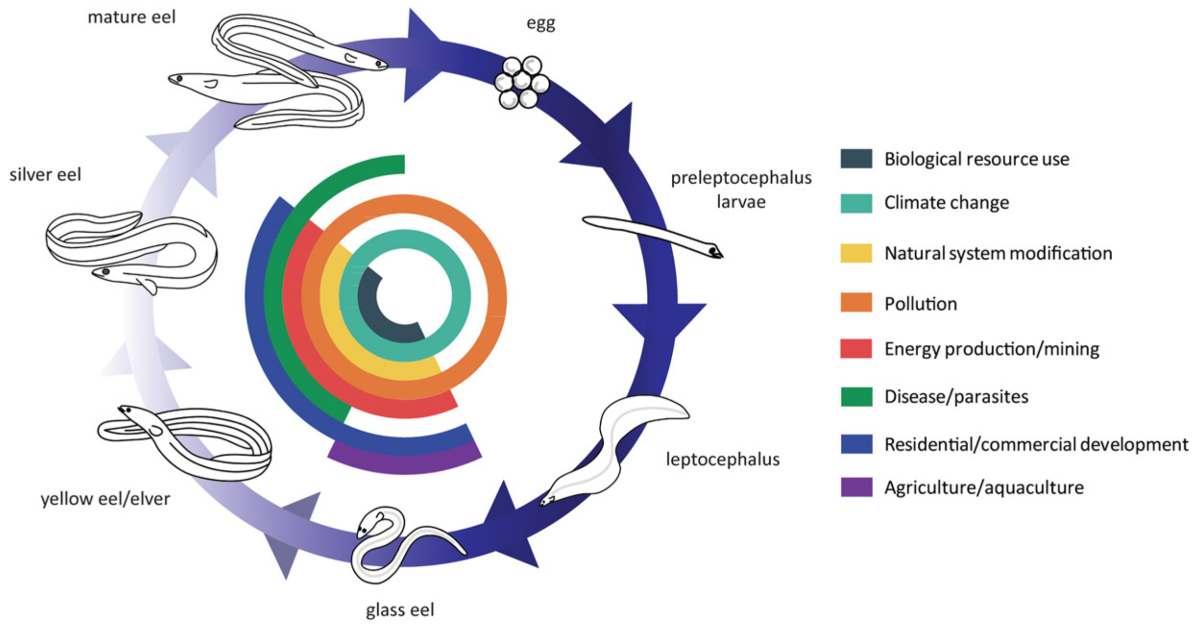

Fig. 4. A schematic diagram of the life cycle of anguillid eels, illustrating how the different life stages are potentially impacted by a variety of threats (using IUCN categories). The darker blue arrows of the life cycle represent the oceanic phases and the lighter blue, the continental phases. Eel illustrations were adapted with permission from Henkel et al. (2012) (1–1.5 columns). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

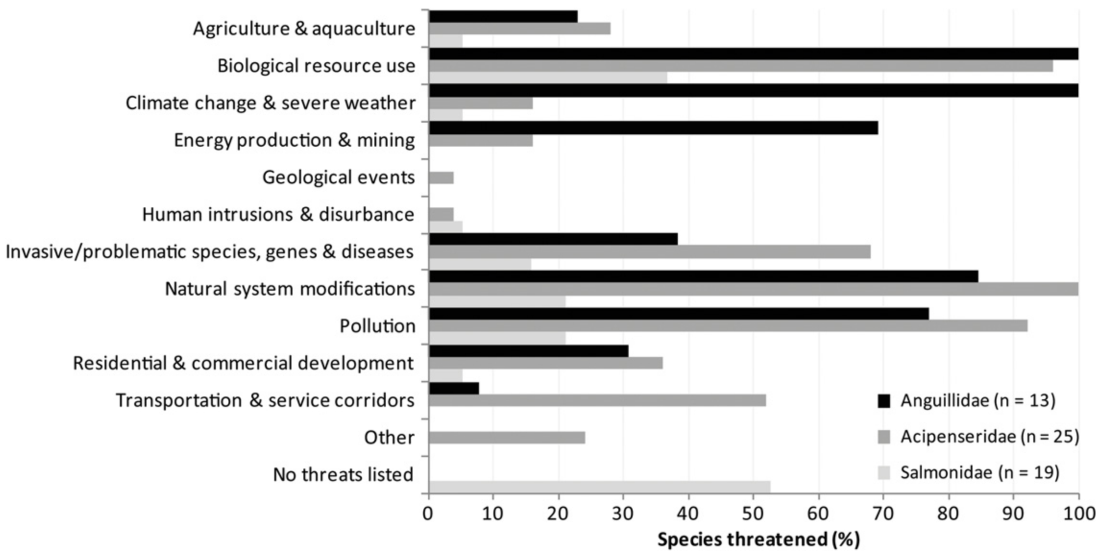

Fig. 5. Comparison of the IUCN Red List coded threats for three diadromous genera, eel (Anguillidae), sturgeon (Acipenseridae) and diadromous members of the salmon family (Salmonidae) based on those species that have been assessed (n). These coded threats are not quantified but rather indicate threats which likely contribute to changes in population dynamics (1.5 columns).

predation by large marine predators such as sharks (Béguer-Pon et al., 2012) and cetaceans (Wahlberg et al., 2014). These latter studies highlight the progress being made towards gaining a better understanding of the oceanic phases of freshwater eels. While the threats do vary between species and with location, the European (CR), American (EN) and the Japanese eels (EN) were found to be subject to all of the above threats which perhaps reflects their imperilled listings but might also reflect the extent and length of the studies on these anguillid eels, relative to others.

3.2. Comparison with other diadromous genera

Despite significant overlap in global range, the distributions of threats across the three diadromous genera (anguillids, sturgeons and salmonids) were considerably different (Fig. 5). Interestingly, the catadromous anguillids were represented by only 13 assessed species but had native ranges spanning 150 different countries, while the anadromous acipenserids or sturgeon species ($n = 25$) and salmonid species ($n = 19$) had continental ranges covering just 43 and 55 countries respectively. While biological resource use impacted a high percentage of both anguillid and acipenserid species, the impact of climate change and energy production/mining threatened a substantially greater proportion of anguillids than either of the other two genera, likely in part, due to the very nature of catadromy. The salmonidae appeared more robust and/or better protected against many of these highlighted threats (Fig. 5).

4. Discussion

Facultatively catadromous, anguillid eels are susceptible to a range of potential threats at every stage of their life history. Although they are a valuable economic resource with substantial ecological and cultural significance in many parts of the world, it is still not fully understood how the multiple threats interact and accumulate to affect the recruiting and spawning stock (Dekker, 2007). While management and conservation initiatives are now in place for some of these species (e.g. European Union Council Regulation (EC) 1100/2007 or the American Eel Recovery Strategy—ICES WKEPEMP, 2013; MacGregor et al., 2013 and ASMFC, 2013), the sustainable use and conservation of anguillids in the future will require cross-disciplinary engagement, integrated management and governance, broad input from numerous stakeholders, and transparency of ideas and materials throughout the process. Since the 2014 Red List assessments were completed, key countries in East Asia have already met to discuss strategies to produce a joint statement in relation to the future of the Japanese eel (http://www.jfa.maff.go.jp/j/saibai/pdf/140917jointstatement.pdf) and other species consumed in these nations, the European eel has been listed on Appendix II of the Convention for Migratory species (http://www.cms.int/en/document/european-eel-anguilla-anguilla-appendix-ii), and fisheries management measures have been implemented in the USA (http://www.asmfc.org/uploads/file//55318062Addendum_IV_American_Eel_oct2014.pdf). With the exception of the three anguillid species that occupy Australasia, this is the first set of global Red List assessments for Anguillidae and the first global analysis of eel population data. In line with the ASSG objectives, these assessments mark the first steps towards the coordinated, international conservation of anguillid eels. Just two of the 13 species assessed were found to be of LC, highlighting that anguillid eels as a whole are in need of intervention, improved management and more detailed monitoring.

4.1. Temperate versus tropical species

According to the assessments the primarily temperate eels from the Northern Hemisphere (*A. anguilla*, *A. japonica* and *A. rostrata*) are by far the most imperilled (Dekker et al., 2003; Dekker and Casselman, 2014) but are also the most well studied while the tropical anguillids, many of which are already Near Threatened, are poorly understood and as such require urgent focus and in most instances increased monitoring (Fig. 2). With trade and exploitation continually shifting comes the growing concern that protective measures banning or restricting the trade of temperate anguillids has, and continues to adjust the focus to some of the lesser-studied tropical species in order to meet the high demand from East Asia (Crook and Nakamura, 2013; Crook, 2014; Nijman, 2015). Indeed, glass eel fisheries for *A. mossambica*, *A. bicolor* and *A. marmorata* have appeared in more remote locations including Madagascar, Reunion Island, parts of Indonesia, Malaysia and the Philippines (FAO, 2013). Yet despite this growing interest, significantly less is known about the population status for most of these tropical eels. Within the Western Central Pacific region in particular, several eel species (*A. celebesensis*, *A. interioris* and *A. luzonensis*) have broadly overlapping ranges and are morphologically difficult to distinguish (Aoyama et al., 2000; Silfvergrip, 2009; Wouthuyzen et al., 2009) and this has resulted in considerable misidentification and uncertainty as to the true geographic ranges of these species. Furthermore, although tropical freshwater eels appear to be characterised by much shorter migration paths to more localised spawning areas (Aoyama et al., 2003), the exact spawning localities for some species remain unknown. In order to better understand these species, the monitoring of tropical freshwater eel recruitment, populations and escapement is essential.

4.2. Knowledge gaps and recommendations

One of the key roles and primary objectives of the ASSG was to highlight gaps in our knowledge that impede the implementation of eel conservation and management. The IUCN Red List process was a fundamental step towards achieving this objective. Analyses of data quality, presented here, promote the recommendation of a continuation and preservation of existing data sets to bring them up to the levels required for increasingly more robust measures of population change. Equally, there were a number of other key recommendations for the genus as a whole that we present here for the first time. Recommendations are in many ways linked and therefore are not listed in any order of importance.

4.2.1. Geographic gaps in the data

A number of regions lacked specialist input and data. These regions included the Gulf of Mexico and the Caribbean – although a recent study begins to address this (see Benchetrit and McCleave, 2015) – large parts of Africa, Central and South Asia, parts of South-East Asia and the islands of the South Pacific. As the exploitation of species in these areas appears to be increasing considerably more monitoring and research is required to effectively mitigate against the potential impact of a shift in fisheries trends. Furthermore, as life history varies substantially across geographic clines, this limited or lack of knowledge about populations in some areas poses the risk that mean generation times for a species, for example, might prove erroneous due to bias from areas where data are available.

4.2.2. Importance of saline water populations

While it is accepted that some individuals within a species spend a significant period of their lives occupying marine coastal habitat, there remains extremely limited information on this marine component of the population and their importance to overall spawning stock (Marohn et al., 2013). Most glass eels enter fresh water, migrating to the upper limits of tidal flow which in the old, flat continents occupied by *A. anguilla* and *A. rostrata* represents exclusively fresh water but for *A. japonica* can be either fresh or brackish water as mountains and the ocean stand adjacent to one another (Kaifu et al., 2010). Once freshwater is detected, this can trigger a range of behaviours: individuals either continue up-river, return to brackish water, or adopt a nomadic life-history where they use a range of saline habitats (Daverat et al., 2006; Cairns et al., 2009). For *A. japonica* for example, it is estimated that 40%–50% of eels in Japan remain in estuarine or saline waters throughout their lives (Kotake et al., 2005; Mochioka et al., 2012) and as such it might be argued that recruitment metrics taken from these environments might be a better proxy of population than attempting to monitor silver eel escapement in these same habitats. Consequently there are significant challenges to the management of this unknown proportion of the population across different species and regions, not least in quantifying their abundance, and while some of the threats discussed may not impact these individuals as significantly, it is probable that they face other threats not influencing the freshwater population. In addition, eel habitat type and quality is thought to play a key role in determining stock declines because of their influence on the quality and reproductive potential of adult spawners (Marohn et al., 2013). Few studies broach this subject and as such, until evidence is available to indicate what proportion of a given population is non-freshwater, we can still only acknowledge its existence. Equally, a proportion of suitable habitat likely remains unfished and unmonitored (Cairns et al., 2014). Despite our lack of knowledge on this, some species' recruitment has reached critically low levels which indicate that any marine element of the population is not buffering the freshwater component sufficiently. Almost all the data that exist pertain to freshwater populations, and it is for these that we are most easily able to implement mitigation actions. With reasonable grounds for concern already, this approach was in line with the Precautionary Principle for species conservation (Darwall et al., 2009; IUCN, 2012b). This does not mean, however, that the importance of salt water populations should be underestimated and, as non-freshwater monitoring improves, this component will need to be built into future assessments.

4.2.3. Oceanography

Anguillid eels are potentially impacted by changes in climate and/or oceanographic processes that influence oceanic events such as *El niño* and the North Atlantic Oscillation. The role these processes play in influencing eel populations is debated (Kimura et al., 2001; Bonhommeau et al., 2008; Miller et al., 2009; Pacariz et al., 2014), not least because so little is known about the marine component of anguillid life histories. Highly pertinent however, is that climate change is most likely to impact individuals during their most critical life stages; the oceanic migration of the larva from the spawning site to their coastal and freshwater growth habitat (i.e. the recruiting population) and the adult silver eel migration from the growth habitat back to their oceanic spawning areas (i.e. the reproductive population). Oceanographic factors (e.g. currents, thermal regimes and increasing acidification) will influence both pre-spawner and larval migrations and survival rates (Miller et al., 2009) and the assessment process could have benefited from the specialist knowledge provided by an oceanographer. Such expertise will prove important for future assessments and it is recommended therefore that the ASSG draws on this for the future assessments.

4.2.4. Silver eel escapement

In the absence of data on the spawning stock of individuals at oceanic spawning localities, silver eel escapement from freshwater or coastal catchments is the most relevant metric for *Anguilla* assessments. However, gathering such data is problematic. The logistical challenges of monitoring out-migration has meant that to date, silver eel escapement data remain relatively sparse (although estimates are increasing for *A. anguilla* from European range states in response to legislation) and until this changes across species (see Fig. 2), available recruitment and yellow eel abundance data serve as the next best proxy for spawning stock. Not without its own difficulties, recruitment is typically monitored at the end of the larval oceanic migration and population dynamics could potentially change significantly from the larval population leaving the spawning area (Melià et al., 2013). Unsurprisingly, there is currently a poor understanding of the relationship between recruitment and spawning stock (Haro et al., 2000; Dekker, 2003; Miller et al., 2009). However, the development of a realistic spawning stock metric for anguillid eels would be a valuable step for future Red List assessments and management of the species. ICES WGEEL is developing a stock–recruitment relationship for *A. anguilla* as a proxy of stock and recruitment index time series

(ICES WGEEL, 2013) with the aspiration that this will allow application of the classical fisheries stock assessment method. It is recommended that this approach be pursued for all species.

4.2.5. Influence of restocked individuals on the population

There is debate as to whether restocked eels (i.e. eels that have been either translocated to new areas or intensively grown out in captivity before being released) contribute significantly to the overall spawning stock biomass for a species (Westin, 2003; Limburg et al., 2003; Westerberg et al., 2014), also making population data analysis more challenging. Indeed recent studies suggest that translocated *A. rostrata* might in fact retain life history parameters (including sex ratios and size at, and timing of, out-migration), comparable with their previous growth or recruitment habitat and thus greater care should be taken to match donor and recipient characteristics (Couillard et al., 2014; Stacey et al., 2014). This debate will be critical to the future management and conservation of all anguillids as at present it is being implemented as a management strategy – as part of EU Eel Management Plans for example – without a full understanding of its effectiveness. It is recommended that the efficacy of restocking as a measure to enhance spawner abundance is determined (note that ICES WGEEL term this the 'net benefit' of restocking).

4.2.6. Extinction risk

The Red List assessments were subject to an extensive peer review process with external reviewers contributing to each species (min–max: 3–11 reviewers). During this process a number of important questions were raised relating to the application of the Red List Categories and Criteria to aquatic species with complex life histories. By definition the IUCN Red List is an assessment of a species' risk of extinction, with listings of VU, EN and CR suggesting that 'best available evidence' indicates that the species is 'facing a high/very high/extremely high risk of extinction in the wild' (IUCN, 2012a). While population trends were not disputed, reviews for species with very broad geographic distributions in particular, questioned the likelihood of actual extinction given the potential carrying capacity of their ranges. Large year-on-year fluctuations in numbers and incomplete knowledge of the population compound this, however, we suggest that increasing use of the Red List as a robust and consistent framework (i.e. species reassessments every five years) will help to highlight and formalise relative change over time.

4.3. Conclusion

Anguillid eels face many threats throughout their long and complex life cycle. The commercial and cultural importance of the three primarily temperate eels (*A. anguilla*, *A. rostrata* and *A. japonica*) has added a political sensitivity to the listing of these species and because of a number of misconceptions about the IUCN Red List process, these assessments can often attract criticism. It is important to note that IUCN themselves state that automatically linking legislative response to a Red List category (e.g. banning trade) is an inappropriate use of the Red List (IUCN, 2014). Here, we present a comprehensive review of the current data trends for anguillid eels, comparing threats with other 'high-profile', diadromous species and suggest priorities for future coordinated international eel conservation. The challenges of applying the Red List process to these ecologically complex species remains; however, we are confident that the broad and meticulous input with which these assessments were assembled, over a two year period, has ensured a rigour that reflects well the current status of the various species. The continued involvement of stakeholders from conservation, governance, industry and academia will be required as sustainability and management strategies are established and developed for *Anguilla* species across the globe.

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Appendix A. Supplementary data

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