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REVIEW

Thirteen novel ideas and underutilised resources to support progress towards a range-wide American eel stock assessment

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Abstract

A robust assessment of the American eel (*Anguilla rostrata*) stock, required to guide conservation efforts, is challenged by the species' vast range, high variability in demographic parameters and data inadequacies. Novel ideas and underutilised resources that may assist both analytic assessments and spatially oriented modelling include (1) species and environmental databases; (2) mining of data from scattered sources; (3) infilling of data gaps by spatial analysis; (4) age estimation from measurements of DNA methylation; evaluation of eel abundance by (5) larval, (6) glass-bottom boat, (7) net enclosure and (8) eDNA surveys; (9) accounting for dam-induced habitat increases in eel watercourse modelling; (10) spatially oriented modelling with and without temporal components; (11)

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geographically nested modelling of glass eel recruitment; (12) spawner per recruit modelling and (13) life cycle modelling to examine larval allocation effects. Eel biologists are too few to gather the required assessment data across all of the species' range. Public posting of electrofishing and eDNA metabarcoding data sets and the use of machine learning techniques to comprehensively inventory small dams will help meet some data needs. These approaches address only a small proportion of the assessment challenges that face American eels. Worldwide collaboration amongst *Anguilla* scientists is a key enabler of progress towards stock assessment goals.

KEYWORDS

eDNA, environmental databases, leptocephalus surveys, maternal philopatry, small ponds, spatial modelling

1 | INTRODUCTION

The American eel (*Anguilla rostrata*) occupies an enormous range in latitudinal (~7000km, Greenland to northern South America), longitudinal (~5000km, Rocky Mountains to the mid-North Atlantic Ocean) and altitudinal (several thousand m, montane streams to 700m ocean depths) spaces (Béguer-Pon et al., 2015; Miller et al., 2015; Shepard, 2015). The 50-million-year history of the genus *Anguilla* adds a time dimension of prodigious duration (Tseng, 2016). Like their congeners, American eels exhibit a multi-habitat and multi-phase life cycle, alternating between the open ocean (migrating and spawning silver eels, eggs and planktonic leptocephalus larvae) and continental waters (glass eels, elvers, yellow eels and developing silver eels). Human interest in American eels is heightened by their commercial value (including lucrative glass eel/elver fisheries), long-standing indigenous cultural links and ongoing biological mysteries (Prosek, 2010).

A key part of the American eel story is genetic structure. The absence of geographic structure in neutral genetic markers between Newfoundland, Canada, and western Florida, US (Bonvechio et al., 2018; Côté et al., 2013; Gagnaire et al., 2012) has led to the widespread conclusion that American eels comprise a single panmictic population. However, a definitive answer on mictic status must await genetic analysis from the vast regions outside the genetically sampled range.

From great ecological success, American and other anguillid eels have fallen into troubled times (Jellyman, 2021). Status reviews have declared American eels to be threatened in Canada (COSEWIC, 2012), depleted in Atlantic US States (ASMFC, 2017) and endangered internationally (Jacoby et al., 2017). In contrast, the US Fish and Wildlife Service (2015) found that the listing of the species in US waters was unwarranted. These reviews accomplished the first level of status evaluation, the cataloguing of threats, that consistently included fisheries overharvest, artificial barriers in fresh water, chemical contamination and introduced parasites. However, firm information is lacking on how these threats impact populations. The second level of evaluation, the compilation and analysis of abundance trends, has shown wide inter-series variation in Canada (Cornic et al., 2021) and in Atlantic

US states (ASMFC, 2017). Declining time series are more numerous than stable and increasing ones, but the dramatic collapse of recruitment to the upper St. Lawrence River and Lake Ontario, widely taken to represent the American eel as a whole (Drouineau et al., 2018), has not been reported elsewhere. The third level of evaluation, analytic stock assessments leading to quantitative benchmarks (biological reference points, BRPs; FAO, 1995), has been developed at local scales (DFO, 2019; Fenske et al., 2011; Weeder & Uphoff, 2009), but the only attempt at a region-scale implementation (Depletion-Based Stock Reduction Analysis for the US Atlantic coast, ASMFC, 2012) was unable to establish BRPs due to multiple data shortcomings (Rootes-Murdy & Anstead, 2019). Difficulties in implementing analytic stock assessments for the American eel have prompted consideration of an alternative approach, in which relations between habitat, distribution and demography are examined by spatially oriented modelling (ASMFC, 2017; Gruss & Thorson, 2019).

Uncertainties in American eel status reviews, and an ongoing sense of conservation peril, have prompted calls for assessment efforts that would pool international expertise, match the geographic scope of the species' presumed single stock and provide robust advice for conservation management (DFO, 2014; Rootes-Murdy & Anstead, 2019). However, a road map for such an endeavour is not apparent. The difficulty of the task is underlined by experience with the closely related European eel (*A. anguilla*). That species has a long history of international collaboration and possesses a much larger knowledge base than does the American eel (5.7× more Web of Science hits for 1960–2020). Nevertheless, European eel management continues to be guided by abundance trends because a robust quantitative assessment has not yet been achieved (ICES, 2021a).

The form of an eventual range-wide American eel assessment is unknown. The premise of this article is that tools to better gather information on American eel distribution and abundance and understand processes that regulate them are likely to aid such an assessment in whatever form it takes. To this end, this article first examines major obstacles that frustrate assessment efforts and then outlines 13 novel ideas and underutilised resources that may help overcome them.



2 | OBSTACLES TO A RANGE-WIDE AMERICAN EEL ASSESSMENT

The American eel's plausible historic continental range, drawn to limits imposed by watershed divides and impassable natural barriers, contains an Atlantic Zone (between Newfoundland and Florida and including the St. Lawrence Basin) and the surrounding Northern (Labrador, Greenland, Icelandic area of hybridisation with the European eel), Western (US Gulf of Mexico drainages) and Southern (Mexico and the Caribbean Basin) Zones (Figure 1). Most, but not all, of the Atlantic Zone is currently occupied by eels (Cairns, 2020). In the other zones, local distributions are poorly known but appear to include numerous unoccupied patches (Shepard, 2015), which can be attributed to migratory obstacles and long distances from the Sargasso Sea spawning area. The Atlantic Zone contains only 20.5% of the species' plausible continental range, but this zone contains all of the species' abundance series, nearly all of the genetic sampling locations used to evaluate the panmixia hypothesis, and most of the source locations for demographic parameters and environmental databases (Table 1, Figure 1). The Atlantic Zone is also the source of nearly all (99.7%) reported yellow and silver eel landings and most (68.3%) reported glass eel and elver landings in 2000–2016 (Cairns, 2020).

Stock assessments require data that represent the stock (Righton et al., 2021). Finding representative data for American eels should be easy because panmictic breeding systems produce genotypes that lack geographically based structure. However, the species' genetic system does not constrain variability but instead facilitates it by high plasticity of gene expression (Côté et al., 2014) and by within-generation spatially varying selection (Babin et al., 2017; Gagnaire et al., 2012; Pavey et al., 2015). These factors together give rise to remarkably high variability in demographic and life history traits.

Known sources of eel trait variation include the following. Temperature impacts on biology, amplified by the American eel's 7000 km latitudinal range, produce a wide variation in growth, mortality and many other demographic characteristics (Jessop, 2010; Vélez-Espino & Koops, 2010). Latitudinal clines may shift ecological traits, such as glass eel run timing (Jessop, 2021). Distance between spawning and growth habitats, ranging from a few 10s to many 1000s of km (Figure 1), affects recruitment opportunities and therefore local population sizes. In northern parts of the Atlantic Zone, American eels in saline water grow at twice the rate and mature in half the time as eels in fresh water (Cairns et al., 2009). Salinity effects on growth and maturity have not been measured elsewhere in the species range. American eel life history differs between sexes, with females maturing 3.7 times older and 4.4 times heavier than males (Cairns et al., 2014; calculations from Cairns, 2020 Supplemental Material Annex B). Growth and mortality rates vary with density (Righton et al., 2021), which also influences the sex ratio by favouring the production of males in high-density areas (Krueger & Oliveira, 1999). In growth experiments with eels sourced from Atlantic estuarine waters, male size distribution varied little, but female growth rate split into slow- and fast-growing clusters (Côté et al., 2015). High levels of inter-individual variation in American eels, unexplained by the above factors, may

arise from sources yet to be elucidated. For example, in European and Japanese (*Anguilla japonica*) eels, variation of growth and trophic level may be linked to behavioural differences related to head shape (termed phrenology, Parker Jones et al., 2018) (De Meyer et al., 2020; Kaifu et al., 2013). American eels exhibit head shape variation (Denny et al., 2012; Hurley, 1972), but its ecological correlates have not been investigated (Morrison & Secor, 2003).

Capturing data across these multiple sources of spatial and other variabilities is a formidable challenge. Demographic data are unavailable in most of the species' range and fall short of properly representing variability even within the relatively data-rich Atlantic Zone. Data-limited assessment techniques (Fukita, 2021) enable assessments with fewer types of data but cannot overcome the requirement that data represent the stock. Anthropogenic mortalities from fishing are documented in official landing statistics. However, directed eel fisheries are absent in most of the Atlantic Zone and in nearly all of the Northern, Western and Southern Zones (Cairns, 2020; Figure 1). Effects of fishing on the stock are difficult to evaluate because the proportion of the stock that is subject to fishing is unknown. Hydroturbine mortality rates can be estimated from passage characteristics (Heisey et al., 2019), but the number of eels that die from turbine strikes is unknown because the number of descending migrants is rarely measured. Barriers to upstream migration, contaminant disruption of reproduction and introduced parasites may also harm eels (Freese et al., 2019; Hitt et al., 2012; Warshafsky et al., 2019), but effects are often diffuse, delayed or uncertain and cannot be readily converted into mortality estimates for quantitative modelling (ICES, 2021c).

In analytic assessments, stock sustainability hinges on a stock's position on a density-dependent stock-recruitment curve (Zhou et al., 2019). Stock-recruitment relations, difficult to measure even in well-studied fish stocks (Lee et al., 2012), have not been demonstrated for American eels (Fenske et al., 2011). An additional complexity for the American eel is that density-dependent effects are likely to vary with local conditions, whilst also influenced by overall recruitment, which is a stock-wide phenomenon (Bevacqua et al., 2019; Righton et al., 2021). The balance of local and stock-wide effects, in turn, influences equilibrium reference points and stock status (Kapur et al., 2021), but this balance is unknown for American eels.

3 | NOVEL IDEAS AND UNDERUTILISED RESOURCES

3.1 | Data sourcing and data tools

3.1.1 | Context

Data for a range-wide American eel assessment are in short supply. This section outlines how data can be obtained from extant sources through public databases and by data mining, and how data processing techniques can sometimes circumvent the need for field data collection.

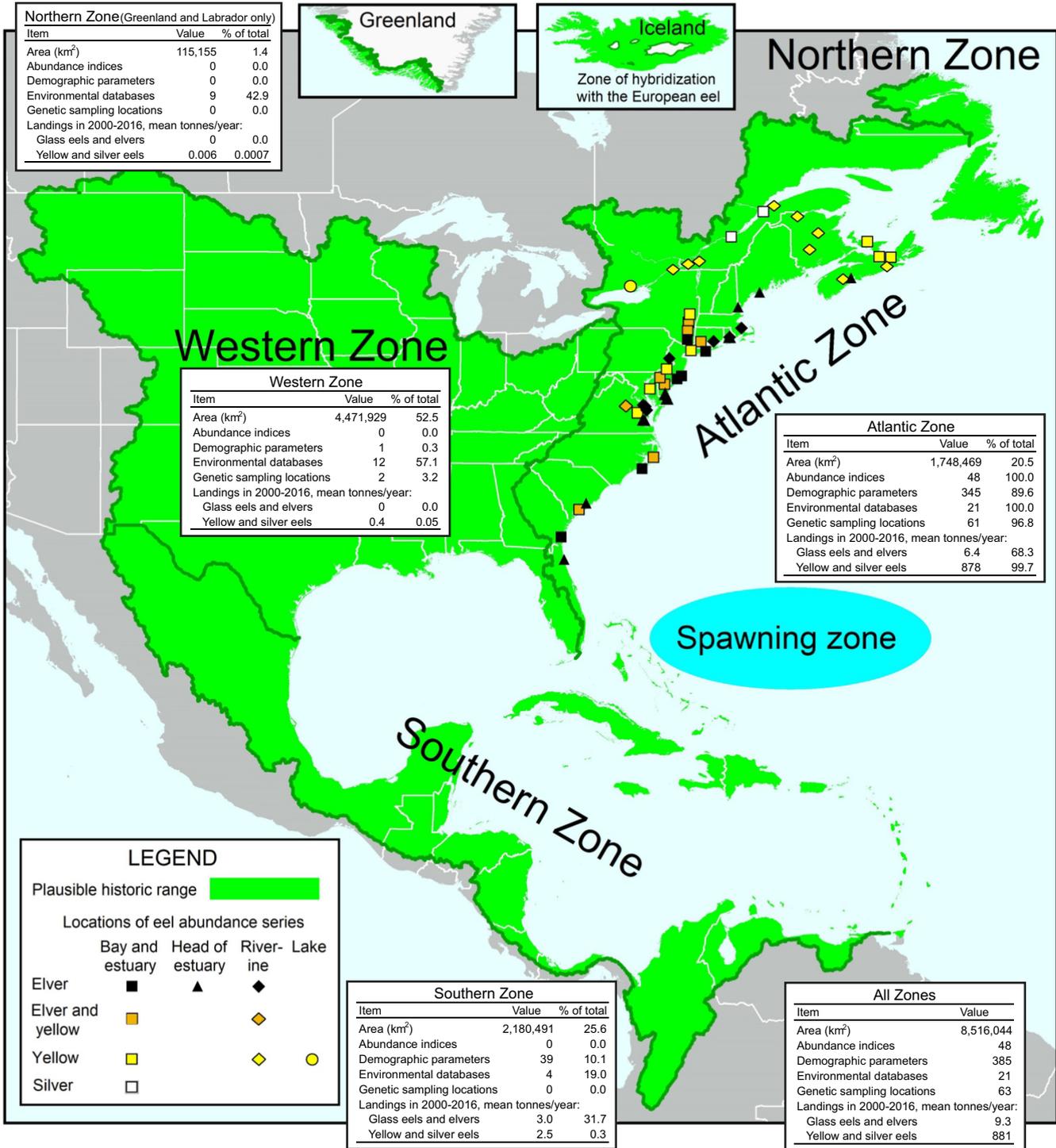


FIGURE 1 Plausible historic continental range of the American eel, drawn from known current distributions up to watershed divides and to impassable natural obstacles. Sources: Spawning zone—Miller et al. (2015); abundance series locations and counts—ASMFC (2012, 2017), Cornic et al. (2021); databases with coverage by zone—Table 1. All other data, including the range map, are from Cairns (2020)

3.1.2 | Use of species and environmental databases

Natural resource information is increasingly being assembled into public databases with broad geographic scope (LaDeau et al., 2017). Many such databases include or potentially include American eel records (Table 2). The Global Biodiversity Information Facility (GBIF),

Biodiversity Information Serving our Nation (BISON) and Ocean Biological Information System (OBIS) draw their information from scientific sources and some contain detailed metadata on individual records. The Aquatic eDNA Atlas accepts data gathered under standardised protocols (Isaak et al., 2018) but has limited coverage within the American eel range. In addition, large amounts of data



TABLE 1 Environmental databases that may aid progress towards a range-wide American eel stock assessment

Theme	Database	Location	Sal. ^a	Comments	Source
Hydrography	Hydrosheds	World	F	Watersheds, river networks, drainage directions	Lehner and Grill (2013), hydrosheds.org
Hydrography	National Hydro Network	Canada	F	Inland water features	open.canada.ca/data/en/dataset/a4b190fe-e090-4e6d-881e-b87956c07977
Hydrography	National Watershed Boundary Dataset	US	F	Watershed boundaries	nhd.usgs.gov/wbd.html
Bathymetry	General Bathymetric Chart of the Oceans (GEBCO)	World	S	Grid of 15 arc-sec (about 0.5 km at the equator)	gebco.net
Bathymetry	Non-navigational bathymetry (NONNA)	Oceans bordering Canada, Great Lakes	F, S	Soundings spaced as close as 10 m	gcgeo.gc.ca/geonetwork/metadata/eng/d3881c4c-650d-4070-bf9b-1e00aabf0a1d
Bathymetry	Olex NL database	Newfoundland and Labrador shelves	S	Crowd-sourced from fishers, 75 m grid	Novaczek et al. (2019)
Bathymetry	Coastal National Elevation Database (CoNED)	Parts of US Atlantic and Gulf of Mexico coasts	F, S	Seamless elevation and depth maps	topotools.cr.usgs.gov/topobathy_viewer/
Habitat	Appalachian-Acadian stream classification	Parts of E Canada and NE US	F	Rivers and streams classified by size, gradient, temperature, alkalinity, tidal influence	2c1forest.databasin.org/documents/documents/43ab64ee3f4a421c96b957f6c563bd/
Habitat	StreamCat, LakeCat	US	F	Flow relations and environmental characteristics for 2.7 million stream segments and 378,000 lakes	Hill et al. (2016), epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys
Habitat	Stream classification system	US E states	F	Classification of reaches by hydrology, temperature, size, gradient. Also fish and macroinvertebrate records	McManamay et al. (2018)
Habitat	National Wetlands Inventory	US conterminous states	F, S	Hierarchical classification of rivers, lakes, ponds and vegetated wetlands	Dahl (2011)
Habitat	Fish Habitat Conservation Area Mapping and Prioritisation Project	Atlantic US interior and inshore waters	F, S	Physical habitat by catchment in fresh water and by 1 km ² hexagons in saline water	atlanticfishhabitat.org
Habitat	West Atlantic Fetch Atlas	E coast of Canada and the US	F, S	Mean fetch calculated for 54,554,794 cells (50 × 50 m up to 5 km from the coast, 200 × 200 m to the 500 m isobath)	D. Cairns (unpublished data)
Barriers	Global Georeferenced Database of Dams (GOODD)	World	F	38,667 records of medium and large dams, from Google Earth analysis	Mulligan et al. (2020), globaldamwatch.org
Barriers	Open Street Maps (OSM)	World	F	>50,000 features that are tagged as dams	openstreetmap.org
Barriers	Inventory of Large Dams in Canada	Canada	F	1157 records of dams, generally >15 m high or impounding >3 million m ³ of water	cda.ca/dams-in-canada/dams-in-canada
Barriers	Quebec dam inventory	Quebec	F	8431 records of dams >1 m high	cehq.gouv.qc.ca/barrages

(Continues)

TABLE 1 (Continued)

Theme	Database	Location	Sal. ^a	Comments	Source
Barriers	National Inventory of Dams/National Anthropogenic Barrier Dataset	US	F	NID documents 92,071 dams, generally ≥ 7.6 m high or impounding $\geq 61,674$ m ³ of water. NABD maps NID dams on stream flowlines	nid.sec.usace.army.mil/sciencebase.gov/catalog/item/56a7f9dce4b0b28f1184dabd
Barriers	Appalachian-Acadian Aquatic Connectivity Tool	SE Canada, NE US	F	Stream barriers and potential barriers (4901 dams, 490 waterfalls, 114,797 road crossings)	2c1forest.databasin.org/galleries/1b5e7612ead34f3a9880a696924bc91e/
Barriers	Freshwater Network Barrier Database	E US, ME to WV	F	13,889 records of dams	freshwaternetwork.org/projects/aquatic-barrier-prioritization/
Barriers	Southeast Aquatic Barrier Database	25 states in central, S and SE US, Puerto Rico	F	391,020 records of dams	connectivity.sarpdata.com

^aSalinity: F, fresh; S, brackish or salt.

relevant to eel distributions, in particular most stream electrofishing series, remain web inaccessible. Where public databases are lacking, researchers have the option of building their own through data mining approaches (see next section).

We identified 21 environmental databases that may assist American eel stock assessments (Table 1). Databases that map watershed boundaries are available for Canadian, US and world fresh waters. Soundings used for nautical charting are increasingly being made publicly available. The Canadian non-navigational bathymetry data set provides soundings at intervals as close as 10 m, although coverage and point spacing are variable. The expanding use of lidar technology has facilitated high-resolution seamless mapping of land elevation and water depths in several stretches of the US East and Gulf of Mexico coasts.

Databases also document key habitat parameters, such as gradient, temperature, flow characteristics and connectivity, of streams and rivers in the US and parts of eastern Canada (Table 1). The US National Wetlands Inventory, which covers open waters as well as vegetated wetlands, provides the most detailed aquatic habitat classification available in the American eel range (Table S1) but contains no information on connectivity. The degree of shelter from the open sea strongly influences the distribution of many marine biota, including eels (Cairns et al., 2017; Pardal et al., 2021). A database (Figure S1) maps the degree of shelter as mean wind-adjusted fetch at 50 m resolution inshore and 200 m offshore for coastal and continental shelf waters of eastern North America.

Dams and other artificial barriers to stream and river flow are documented in databases with regional to worldwide scope (Table 1). However, databases concentrate on medium and large dams, leaving most of the several million small dams in the US uninventoried (Table 3 and Table S1). A newly developed machine learning algorithm, used to identify dams in Southeastern New York State, indicated that 80%–94% of dams were previously undocumented by any database (Buchanan et al., 2022). Small dam density in US Atlantic states, based on counts of 0.5–40 ha ponds on 1:24,000 scale maps (Fleming & Stubbs, 2012) and the assumption that two-thirds of ponds are formed by dams (Renwick, 2017), is 0.423 dams/km² (Table S2). This dam density is 4.3–19.1 times higher than dam densities calculated from eastern US dam inventories that were created to guide the restoration of connectivity in river systems (Table 1). This differential implies that dam inventories overlook most dams in river systems within their coverage areas.

Crowd sourcing increasingly populates public databases. iNaturalist accepts species (including American eel) records from citizen scientists. Open Street Maps posts volunteer-supplied dam records, although coverage is sparse in the American eel plausible range (Table 1, osm.org). In Europe, a consolidated barrier inventory containing ~640,000 records is believed to be missing many dams. Citizens are helping to add missing dams via a smartphone application (Belletti et al., 2020; amber.international). Crowd-sourced soundings were used to map the bathymetry of Newfoundland and Labrador shelves at higher spatial resolution than official charts (Novaczek et al., 2019).



TABLE 2 Species databases that show or potentially show American eel records

Database	Location	Salinity ^a	Number of American eel records	Comments	Source
Ocean Biodiversity Information System (OBIS)	All	F, S	15,590	Aggregated from numerous databases. Currently expanding to include eDNA records	obis.org
Global Biodiversity Information Facility (GBIF)	All	F, S	9691	From research-grade sources. Currently expanding to include eDNA records	gbif.org
Biodiversity Information Serving our Nation (BISON)	US	F, S	12,163	Includes records from GBIF	bison.usgs.gov
Aquatic eDNA Atlas	Western US, part of the Appalachian region	F	3	Crowd-sourced from researchers	www.fs.fed.us/rm/boise/AWAE/projects/eDNAAtlas/the-edna-atlas-results.html
IchthyMaps	US	F	3241	Compiled from fish atlases	Frimpong et al. (2016)
iNaturalist	All	F, S	1248	From citizen submissions	inaturalist.org

^aF, freshwater; S, salt and brackish water.

TABLE 3 Number and area of US lakes and ponds, including lakes and ponds formed by dams (headponds)

Region	Lakes and ponds			Comments	Source
	Number	Area (km ²)	Habitat type		
All US	2,000,000		Headponds	Formed by dams impounding <61,674 m ³ of water	US ACE, unpublished data quoted by Graf (1993)
All US	6,570,000		All lakes and ponds		Renwick (2017)
All US	2,600,000	21,000	Non-riverine water bodies	0.06 -1 ha, from satellite images	Smith et al. (2002)
All US	21,600		Small ponds		Downing et al. (2006)
Conterminous US	4,540,284	30,267	Small ponds	Ponds between 0.5 and 40 ha	Fleming and Stubbs (2012)
Atlantic states	720,207	6650	Small ponds	Ponds between 0.5 and 40 ha	Fleming and Stubbs (2012)
Atlantic drainages		3078	Palustrine (pond) habitat		Dahl et al. (2009) as compiled by Cairns et al. (2014)

3.1.3 | Mining of data from scattered sources

Where public databases fall short of needs, researchers have the option of building their own. Using a data mining approach, American eel range edges in Mexico and the Caribbean Basin were clarified by searching records from museums, checklists and grey literature, followed by contact with local experts and in some cases museum visits to verify specimen identities (Benchetrit & McCleave, 2016). This approach achieved the first reliable account of eel distribution in an area where formal ichthyofaunal surveys were rare. Similarly, early distributions of European eels on the Iberian Peninsula were mapped from historic records (Clavero & Hermoso, 2015). Another data mining approach is to assemble quantitative survey data from dispersed sources, such as an electrofishing database for US mid-Atlantic states that was built by simply asking fisheries agencies for their records (Lapointe et al., 2016). Similarly, data from 26 trawl and beach seine surveys were assembled to map detections and catch rates of American eels in marine waters between Labrador and Florida (Figure S2; Cairns et al., 2017). Some input surveys were widely cited in peer-reviewed literature, whereas others were web invisible and only discovered by direct inquiries to data-holding agencies. Many additional surveys, not compiled in any database, may provide additional information on American eel marine distribution (Table S3; Figure S2).

Organisations may be able to canvas potential data sources more thoroughly than individual researchers. For example, a consortium of private and public stakeholders in France, Spain and Portugal (SUDOANG) compiled a comprehensive set of eel-relevant data from heterogeneous databases (Mateo et al., 2022).

3.1.4 | Infilling of life history parameter gaps by spatial analysis

The vast extent of the American eel's continental range (Figure 1) dictates a need for location-specific life history parameter estimates in a range-wide stock assessment. Parameter estimates are heavily concentrated in the Atlantic Zone (93 of 94 parameter territory cells; Cairns, 2020). However, even in this relatively data-rich zone, 38% of parameter territory cells lack local data.

Life history parameters in the Atlantic Zone are related to temperature (associated with latitude), distance from the Sargasso Sea spawning area (DSA) and salinity (Cairns, 2020; Cairns et al., 2009, 2014; Jessop, 2010; Vélez-Espino & Koops, 2010). For example, silver eel length varies little with latitude south of Cabot Strait but increases with increasing DSA beyond it. Female growth rates south of Cabot Strait decrease with latitude and DSA in fresh but not in saline waters. These patterns suggest that clinal relations between life history parameters and geographic and environmental factors could fill spatial data gaps (Vélez-Espino & Koops, 2010). However, a simple infilling rule (statistically significant clinal relations, interpolation but not extrapolation) infilled only one parameter

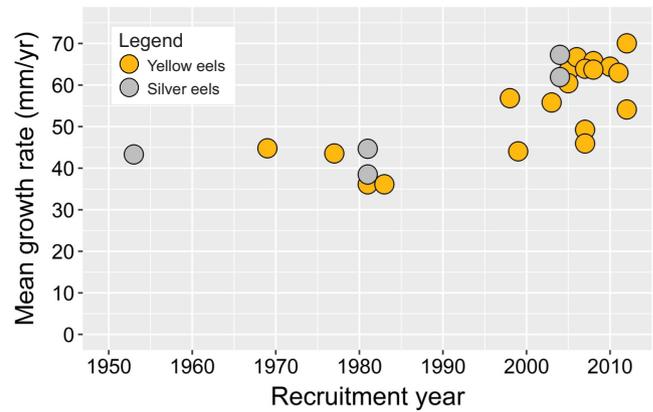


FIGURE 2 Mean growth rates of naturally migrating yellow and silver eels in the St. Lawrence Basin between recruitment to continental waters and the year of sampling, in relation to recruitment year. Data are from Table S4

territory cell (Cairns, 2020). Spatial modelling by empirical orthogonal functions has been used to map demographic variation in marine fish from physical data (Gruss et al., 2021). This approach may offer a more effective means to fill spatial gaps in American eel parameters.

The most pressing data need for a range-wide American eel assessment is not to fill gaps in the Atlantic Zone but rather to obtain inputs for the Northern, Western and Southern Zones. Expansion from the first points of field data collection, and infilling by spatial analysis techniques, may, with time, achieve the broad data coverage that a range-wide assessment requires.

3.1.5 | Age estimation without otolith reading

Age composition is a critical source of information for understanding fish population dynamics (Hilborn & Walters, 1992). Scale-based age estimation, preferred because of its simplicity and harmlessness to fish, is unsuitable for American eels because their scales first appear when they are several years old (Smith & Saunders, 1955). Hence, eel age must be estimated from otoliths, which requires lethal sampling and labour-intensive specimen preparation (ICES, 2020b). In contrast, lengths of live eels can be efficiently measured without anaesthetic using a V-shaped measuring trough (Figure S3). However, high individual variability in anguillid eel growth rates precludes a simple predictive relation between length and age.

Length frequency analysis (LFA) decomposes length frequency distributions into age distributions to reveal age-based modes that are not apparent by visual inspection (Macdonald, 1987). LFA uses a training data set of lengths and ages to derive a function that estimates age structure from samples in which only length has been measured. LFA was used to estimate the age of eels ascending the Saunders ladder on the Moses-Saunders Dam on the upper St. Lawrence River, using the length and age of eels sampled during 2006–2008 for training (Zhu et al., 2013). Despite high variation

in length at age (Figure S4), LFA successfully converted lengths to ages, enabling the calculation of cohort strengths for year classes between 1967 and 2005.

Length frequency analysis assumes that training and length-only data sets have similar length-at-age structures. The first precaution in its application to eels is that training and length-only data sets should be from the same region and habitat, to avoid latitudinal (Jessop, 2010) and salinity-based (Cairns et al., 2009) variation in eel growth. However, eel growth rates may also vary over time at the same location. Eel growth is affected by temperature (Cairns et al., 2014), which may increase with global warming, and by density, which may affect growth rate directly (Bevacqua et al., 2019) and also alter sex ratios, which changes growth rate by shifting the balance between fast-growing females and slow-growing males (Jessop, 2010). European eel growth in western Ireland changed non-linearly with temperature over seven decades (Vaughan et al., 2021). In western France, the median length at age of eels <6 years doubled between the early 2000s and the early 2010s (Patey et al., 2018).

To test for American eel growth variation in the St. Lawrence Basin, mean growth rates of 24 yellow and silver American eel samples were plotted against the year of recruitment (Figure 2, Table S4). Eels that were recruited between the 1950s and the 1980s grew at stable rates, but the growth rate rose markedly in eels recruited after the late 1990s. This rate increase may have been a density-dependent response to the collapse of eel populations in the upper St. Lawrence in the 1990s (Cairns, 2020). The training set sampled in 2006–2008 (Zhu et al., 2013) would have recruited in the early 2000s, about the time growth rates were increasing. This means that the LFA function developed by Zhu et al. (2013) would give unreliable results if applied to subsequently measured eel lengths.

Length frequency analysis estimates eel age structure without costly and intrusive otolith age estimation. However, the temporal growth variation found in the St. Lawrence and elsewhere points to the need to verify growth rate stability before the method can be reliably applied. This problem is circular in nature because otolith-based age estimation is required to test for growth stability. If ages are estimated from otoliths, there is no need for LFA.

Measurement of DNA methylation has recently emerged as a promising technique for fish age estimation. The proportion of certain cytosine bases within the DNA molecule that bear attached methyl groups changes with clock-like consistency (Anastasiadi & Piferrer, 2020). Methylation frequency has been found to predict independently measured age of both wild and captive-reared fish with high degrees of explained variance (Mayne et al., 2021; Weber et al., 2022). DNA methylation can be measured cheaply in samples collected non-lethally (e.g. fin clips). With appropriate validation, American eel age estimation by DNA methylation could potentially become widespread and routine, to the benefit of many types of quantitative analysis that require age inputs.

3.2 | Field methods to determine distribution and abundance

3.2.1 | Context

A robust assessment of American eel stock status requires knowledge of where eels are found and not found. Distribution is poorly known in the Northern, Western and Southern zones, where a sizeable fraction of the range marked “plausible” (Figure 1) may be unoccupied by eels (Shepard, 2015).

Assessments also require information on relative and absolute abundance. In shallow lotic (flowing river and stream) habitat, backpack electrofishing is commonly used to determine the distribution and abundance of yellow eels (Reid, 2011). Lentic (non-flowing) waters are a major growth habitat for eels (Trancart et al., 2018), but abundance measurements are more difficult. Mark-recapture experiments may fail to obtain the minimum of recaptures needed to produce estimates with reasonable confidence levels (Diekmann et al., 2019; Jellyman & Crow, 2016) (Table 4). In unbounded systems (large lakes, estuaries and bays) conversion of mark-recapture population estimates to densities is uncertain due to difficulties in establishing effective home range size (Walker et al., 2014). In marine waters, trawl monitoring programmes have produced a wealth of data indicating eel distribution (Cairns et al., 2017). However, trawls do not supply density estimates because trawl catchability is unknown (Cairns et al., 2017). Boat electrofishing uses boom-mounted electrodes to flush and partially stun eels, so they can be dip-netted for counting and measurement (Casselmann & Grant, 1998; Lloyst et al., 2015). Because stunned eels must be seen (usually with the aid of lights, at night) to be caught, the method requires clear water and calm conditions. Efficiency decreases with water depth, thereby causing an unquantified bias that reduces the reliability of density estimates (Meulenbroek et al., 2020). Boat electrofishing is used in two American eel abundance series (Lake Ontario, South Carolina estuaries; Figure 1). Boat electrofishing is effective only in low salinity waters (<10 ppt, ASMFC, 2012), but technological developments are extending its application into brackish areas (Lieschke et al., 2019).

This section outlines methods that potentially measure distribution, relative and absolute abundance, and temporal abundance change of American eel larvae in the open ocean (trawl surveys), yellow eels in lentic waters (glass-bottom boat surveys and net enclosures) and all stages in all habitats (eDNA).

3.2.2 | Abundance from larval surveys

The establishment of an overall abundance trend for American eels is challenged by heterogeneous trajectories of glass and yellow eel time series (ASMFC, 2017; Cairns, 2020) and because silver eel abundance has been monitored in only one watercourse (the St. Lawrence River, Figure 1). Measurements of larval abundance



TABLE 4 Comparative capacities of established and novel survey methods to estimate American eel densities in lentic (non-flowing) waters

Method	Type ^a	Usual time ^b	Requires visibility to the bottom	Salinity ^c	Comments	Sources
Mark-recapture	E	N	No	F, B, S	Large sampling effort is needed to obtain sufficient recaptures to produce population estimates. The unbounded nature of bays and estuaries poses difficulties in converting populations to densities	Diekmann et al. (2019), Walker et al. (2014)
Trawling	E	D, N	No	F, B, S	Eels caught per swept area cannot be converted to densities because capturability is unknown and probably low	Cairns et al. (2017), Van De Wolfshaar et al. (2014)
Boat electro-fishing	E	D, N	Yes	F, B	Calm conditions are required to avoid surface ripples that distort vision into the water. Limited to waters with salinity <10 ppt, although equipment suitable for higher salinities is under development	ASMFC (2012), Lieschke et al. (2019)
Glass bottom boat surveys	N	N	Yes	F, B, S	The viewing window flattens the water, making visibility independent of wind. Underestimates true density because an unknown proportion of eels are concealed in the substrate	Cairns et al. (2009), ICES (2009)
Net enclosures	N	N	No	F, B, S	Density estimation by the depletion method assumes no ingress or egress across the boundary net. This assumption is often unmet	Dorow et al. (2020), Ubl and Dorow (2015)
eDNA	N	D, N	No	F, B, S	Can provide presence detection in all habitat types over very large areas at low cost. The capacity of eDNA to indicate abundance is advancing	Miya (2022), Yates, Cristescu, et al. (2021), Yates, Glaser, et al. (2021)

^aE, established; N, novel.

^bUsual time at which eels are caught or detected. D, day; N, night.

^cF, fresh; B, brackish; S, salt.

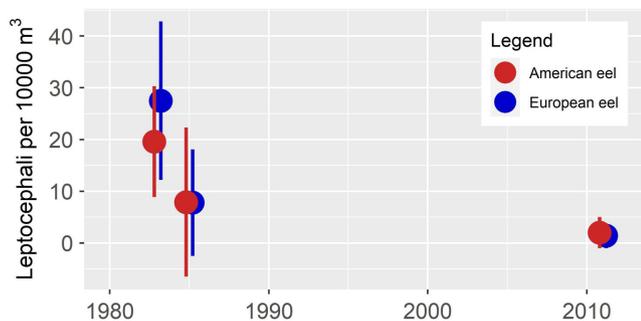


FIGURE 3 Mean (\pm SD) number of American and European eel leptocephali caught per 10,000 m³ of water filtered in Isaacs-Kidd midwater trawls in the Sargasso Sea in 1983, 1985 and 2011. The position of symbols on the horizontal axis is offset to reduce overlap. Data from Hanel et al. (2014)

in the Sargasso Sea spawning area provide an opportunity to generate a single index that reflects the whole stock. Indices of American and European eel leptocephali in the Sargasso Sea (numbers per 10,000 m³ of water filtered by Isaacs-Kidd Midwater Trawl) declined by 60% and 82%, respectively, between 1983 and 1985, and by 75% and 79%, respectively, between 1985 and 2011 (Hanel et al., 2014) (Figure 3). Catch rates were significantly lower in 2011 than during 1983–1985 (*t*-tests, $p < 0.001$). However, this comparison could be biased by differences in sampling gears and oceanographic features between the two periods. In contrast to declines of the two *Anguilla* species, no consistent trends were observed for other anguilliform leptocephali sampled by the same method (Hanel et al., 2014). Reported *Anguilla* declines are hence unlikely to be measurement artefacts. Survey catch rates of European eel leptocephali from 1920 to 2014, converted to a standardised measure, also indicated a decline in that species (Westerberg et al., 2018). Analyses of this type have not been conducted for the American eel.

Measured American eel leptocephalus concentrations differed substantially between 1983 and 1985 (Figure 3), thereby suggesting high biological variability or high sampling error. The use of a larval time series as an abundance indicator would prompt questions of its quantitative relation to preceding and subsequent life stages. Larval series might hindcast spawning biomass and spawning output, but this relation could be affected by possible delayed mobilisation of toxic chemicals that impair the formation of viable eggs and milt (Belpaire et al., 2019). Larval series might forecast glass eel recruitment, but this relation could be affected by shifts in Gulf Stream warm-core eddy patterns that might either aid or hinder transport to continental coasts (Jessop, 2020). When published, findings of Sargasso Sea larval surveys conducted by the Thünen Institute of Fisheries Ecology (Bremerhaven, Germany) in 2014, 2015 and 2017 will extend the time series of larval abundance (R. Hanel, Thünen Institute, personal communication). A first post-COVID cruise is anticipated for 2023, with subsequent cruises at 3-year intervals.

3.2.3 | Abundance from glass-bottom boat surveys

Mark-recapture has furnished 14 American eel density estimates for fresh and saline lentic waterbodies in the southern Gulf of St. Lawrence (Table S5), but intense labour requirements (mean project duration 64 days) prompted a search for a time-efficient alternative suitable for all salinities. Glass-bottom boat surveys can be considered a variant of dive surveys (Schulze et al., 2004; Ward-Paige et al., 2010), in which the dive mask is replaced by a viewing window, with the key difference that working in air circumvents limits of diver endurance and facilitates the use of electronic assists (e.g. voice recorders and GPS tracking systems). Glass-bottom boat surveys were conducted at night in a 4-m boat fitted near the bow with a triangular hull window (103 cm wide, 62 cm high) and six LED lamps mounted on an underwater shelf, which also served to divert bubble-laden surface water away from the viewing window (Cairns et al., 2009; ICES, 2009; Figure S5). A prone observer counted eels within transects delimited by stretched cords on either side of the window. Surveys were conducted to maximum depths of 2.5–4 m, in spring, before algae blooms impaired visibility. Densities were calculated as counts divided by transect area and confidence limits were calculated by a bootstrap technique (ICES, 2009). Thirty-nine one-night surveys were conducted, yielding density estimates with confidence intervals broadly similar to those produced by the more labour-intensive mark-recapture method (Table S5).

Glass-bottom boat surveys and boat electrofishing both require visibility to the bottom. The glass-bottom window smooths surface ripples, enabling surveys in up to moderate winds, whereas boat electrofishing requires calm conditions to permit visibility through the water surface (Table 4). Both methods underreport true density if some eels are concealed in the substrate or bottom debris. Telemetry has shown that eels are commonly inactive for extended periods at night, despite an overall nocturnal activity cycle (Barry et al., 2016; Walker et al., 2014). However, inactive eels are not necessarily concealed because most (72%) eels encountered during glass-bottom boat surveys laid motionless just above the substrate (Hallett, 2013). Given the uncertainties attending concealment bias, glass-bottom boat density estimates must be considered minima. In boat electrofishing, the risk of missing concealed eels is reduced by the flushing behaviour of shocked eels, although the proportion that does not flush has not been measured.

3.2.4 | Abundance from net enclosures

In coastal waters of the German sector of the Baltic Sea, yellow European eel abundance is estimated by net enclosure surveys (Ubl & Dorow, 2015). An area of 100 m × 100 m (1 ha) is enclosed by a 1.8-m high boundary net, with 10-mm mesh size. Fyke nets are set in each corner and in six chains within the enclosure. Nets are fished for 48 h, after which the enclosure is removed. With a crew of three and two complete enclosure systems, four locations (i.e. 4 ha) can be sampled per working week.

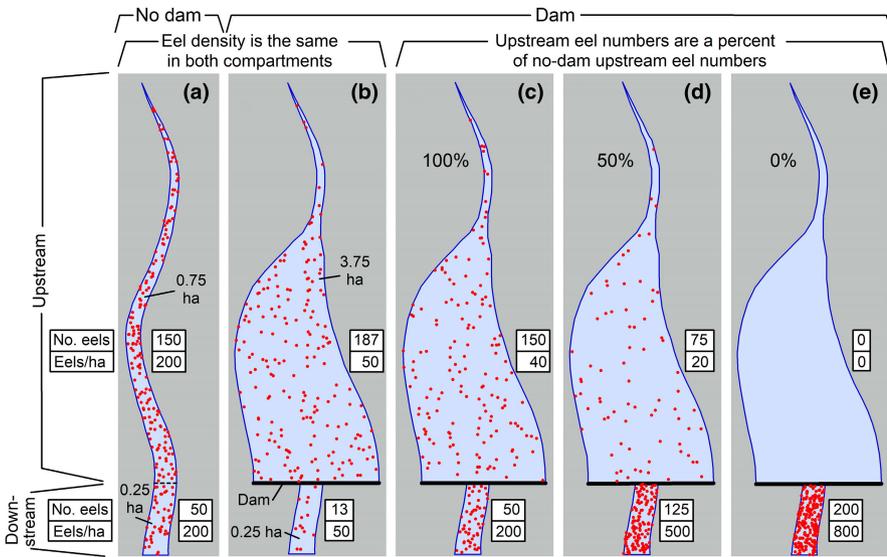


FIGURE 4 Scenarios in which 200 yellow American eels occupy a watercourse without (a) and with (b–e) a dam. Eel distribution is random within each compartment. (a, b) Eel density is the same in upstream and downstream compartments. (c–e) Eel numbers in the upstream compartment are 100%, 50% and 0%, respectively, of upstream numbers in the no-dam scenario (a)

Because boundary net float lines are typically below the water surface, eels are capable of entering or exiting the enclosure. A telemetry study in 3 m of water found that enclosed eels moved along, or away from, the boundary net, but that 43% of non-recaptured eels left the enclosure within 48 h (Dorow et al., 2019). However, this study was conducted without fyke net chains, which are responsible for 79% of eel captures in standard enclosure deployments. Hence, escapement in the standard protocol would likely be less than 43%. Hierarchical Bayesian modelling of a three-pass removal experiment (fishing at 48, 72 and 96 h) indicated that a mean of 39% of enclosed eels >36 cm was captured after 48 h of fishing time (Dorow et al., 2020). The inverse of 39% (2.6) can be used as a raising factor to convert 48 h eel catches into densities (eels/ha).

The enclosure method has also been tested in lakes and a lagoon in Ireland (R. Poole, Marine Institute, Newport, Ireland; personal communication), Estonian lakes (P. Bernotas, Estonian University of Life Sciences; personal communication), a French river (Allou et al., 2018) and a Mediterranean lagoon (E. Amilhat, University of Perpignan; personal communication). Conversion of eel catches to densities by the removal method requires the assumption that the enclosure protects against eel entry and exit, so that catch per unit effort (CPUE) declines with progressive depletion of eels within the enclosure (Table 4). These trials have highlighted the need to deploy enclosures where habitat characteristics (shallow depth, even bottom, low or no current) reduce the frequency of eel movement across the boundary net.

3.2.5 | Distribution and abundance from environmental DNA

The detection and measurement of DNA that organisms release to the environment has become a powerful tool in aquatic biodiversity assessment (Deiner et al., 2021). The eDNA method involves the collection of water samples that are filtered and amplified by polymerase

chain reaction (PCR) to detect (qPCR) or identify (metabarcoding) genetic material. qPCR provides sensitive presence detection for single species and also measures eDNA concentrations that are increasingly used to infer the abundance of wild populations (Kasai et al., 2021). Metabarcoding detects multiple species by using primers to amplify DNA barcode regions, followed by high-throughput DNA sequencing to yield information on community composition and species distribution (Deiner et al., 2017; Miya, 2022).

In eDNA studies, the replacement of labour-intensive animal capture by simple water collection increases field efficiency. For American eels, this efficiency gain opens a path towards broad geographic data coverage that is needed for a range-wide stock assessment. In much of the Northern, Southern and Western Zones, local distributions are poorly known. Metabarcoding studies can help fill these gaps by detecting eel presence without the need to commission eel-centric investigations. However, such records need to be accessible to be useful. The Aquatic eDNA Atlas assembles eDNA-based presence data but covers only a small portion of the plausible American eel range (Table 2, Figure 1). The expansion of the OBIS and GBIF biodiversity platforms to include eDNA data aims to address eDNA data accessibility issues on a worldwide scale (Andersson et al., 2021).

American eel densities, a valuable parameter in stock assessments, are available only in scattered locations (Table S5). eDNA concentrations change with seasonal cycles of eDNA release, and degradation dispersion varies with physical and chemical water characteristics and currents (Caza-Allard et al., 2022; Kasai et al., 2020; Laporte et al., 2020; Takeuchi et al., 2019). eDNA concentrations explained 57% of the variation in estimated aquatic species abundance in 25 studies conducted in natural waters (Yates et al., 2019). For anguillid eels, studies have reported low (32%, Japanese eel, Itakura et al., 2019), variable (43%–95%, European eel, Weldon et al., 2020) and high (99%, American eel, Chin et al., 2021) explained variation of abundance estimates. Models that treat eDNA release as an allometric function of body size increase explained variation (Yates, Glaser, et al., 2021).

3.3 | Eels and habitat

3.3.1 | Context

Anguillid eels occupy many aquatic habitats, but they often prefer some habitats over others (Righton et al., 2021). Eels in fresh water typically migrate up watercourses to reach growth habitats. This section presents a conceptual model of how eels distribute themselves in watercourses that have dams, especially small dams that are more likely to permit upstream passage. It also describes the application of spatial modelling techniques to eel habitat use in the eastern US and in New Zealand.

3.3.2 | Determining the net impact of small dams

Many freshwater organisms require connectivity to navigate watercourse axes for their life history needs (Leibowitz et al., 2018). Dams are considered universal villains in anguillid eel conservation by impairing upstream and downstream connectivity (Haro et al., 2000; Woods & McGarvey, 2018) and by killing or maiming descending migrants by hydroturbine strikes (Mensing et al., 2021; Sweka et al., 2014). Nevertheless, several considerations suggest that a broader approach is warranted. First, dams increase aquatic habitat by widening rivers into impoundments and reservoirs. Second, a thread of aquatic science, seldom cited in dam impact literature, argues that small ponds formed by dams (impoundments) provide ecological benefits that justify building more of them (Burger et al., 2018; Neal & Willis, 2012; the UK Million Ponds Projects, freshwaterhabitats.org.uk/projects/million-ponds/). Finally, abundant eel populations sometimes coexist with dams, both small and large. Artificial duck ponds in New Zealand's Southland support high densities of shortfin (*Anguilla australis*) and longfin (*A. dieffenbachii*) eels (Stewart et al., 2021). In the St. Lawrence system, Lake Ontario and Lake Champlain maintained high American eel production for 70 and 140 years, respectively, after the first damming of their outlet rivers (Les Cèdres Dam, main St. Lawrence channel, 1913–1914; St. Ours Dam, Richelieu River, 1846) (Busch & Braun, 2014; Morin & Leclerc, 1998; Verdon et al., 2003).

Small dams rapidly proliferated in Europe about 1000 years ago, fueled by advances in watermill design (Lenders et al., 2016). Watermilling was enthusiastically embraced by European colonists to North America, and a high proportion of stream reaches in the eastern US have been intensively and repeatedly dammed (Walter & Merritts, 2008). Small dams within the American eel range are not accurately inventoried. Small ponds in the US are estimated to number several million, with most formed by dams (Table 3). An estimated 21% of the drainage area of the conterminous US flows through small ponds (Renwick et al., 2005). US Atlantic and St. Lawrence drainages contain 3330 km² of palustrine (pond) habitat (data from the US National Wetlands Inventory, Table S1), most of which is likely formed by dams. In contrast to small dams,

large dams are fewer in number (although each dam backs up more water), newer (mostly constructed in the 20th century; Juracek, 2014), usually contain hydroturbines and are well inventoried (Table 1).

Because passage impairment increases with dam height (Itakura et al., 2020), increased aquatic habitat above large and high dams is generally inaccessible to eels, unless alternate routes (fishways or ship canals) are available. Eels have a better chance of reaching habitat above small dams. Nature-like fishways readily pass eels because they imitate low-gradient natural channels (Tamario et al., 2019). Yellow eels can ascend concrete fishways designed for salmonids but not earthen dams with overhanging spillways (Lamson et al., 2006).

We simultaneously examined the effects of dam passability and dam-induced habitat increases on eel density and distribution in a hypothetical watercourse 1 km long, so that the density decline with distance from the river mouth that occurs in large systems (Ibbotson et al., 2002) could be ignored (Figure 4). The watercourse was colonised by 200 yellow eels which distributed themselves under varying conditions of dam presence or absence and passability. Eel distributions were tested against two benchmarks: (a) constant ascent, in which the number of eels passing upstream of the dam site was the same before and after dam construction, and (b) equal density, in which eels/ha was the same above and below the dam site. Under scenarios of constant ascent (Figure 4a,c), downstream and upstream numbers were unchanged after dam construction. However, dam construction increased upstream habitat from 0.75 to 3.75 ha, thereby leading to an 80% decrease in upstream density, whilst downstream density was unchanged. When eel numbers above the dam were set at 100%, 50% and 0% of pre-dam upstream numbers, numbers and densities progressively decreased in the upstream compartment but progressively increased in the downstream compartment (Figure 4c–e). Under uniform density scenarios, upstream numbers increased and downstream numbers decreased after dam construction, whilst density in both compartments decreased due to increased habitat (Figure 4a,b).

Attainment of passage benchmarks can be gauged from a data set of American eel densities in Prince Edward Island, Canada (Table S5). Mean densities were 142.5 eels/ha (SD = 159.6, $N = 4$) for impoundments and 114.5 eels/ha (SD = 160.2, $N = 35$) for estuaries and bays (ANOVA $F = 0.11$, $p = 0.74$). Densities in impoundments paired with receiving estuaries/bays also did not differ significantly (impoundments: 142.5 eels/ha, SD = 159.6, $N = 4$; estuaries/bays: 130.2 eels/ha, SD = 96.0, $N = 4$; paired t -test, $p = 0.820$). These impoundments thus attained the equal density benchmark of eel passability, which implies that they benefit eels by providing unimpeded access to the additional habitat they create. Otolith microchemistry further suggests that access is bi-directional, with eels readily transiting upstream and downstream across dams (Lamson et al., 2006).

Evaluations of dam impacts on eels assume that stream densities that are lower above than below a dam are caused by passage impairment at the dam site (Camhi et al., 2021; Cooney & Kwak, 2013;

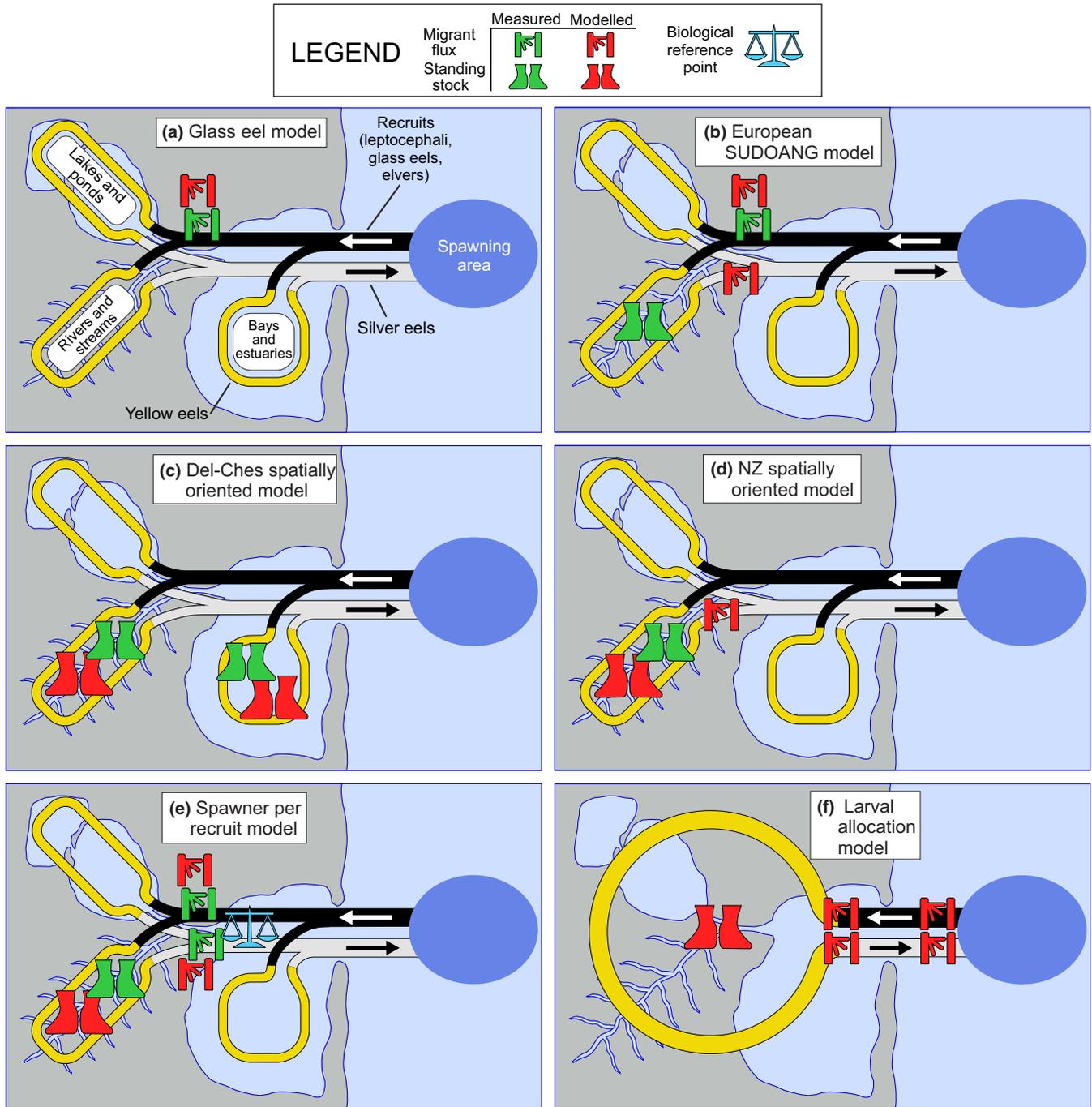


FIGURE 5 A simplified depiction of the anguillid eel life cycle, showing points where migrant flux and standing stocks are measured or modelled in (a) the glass eel model (GEREM), (b) the European SUDOANG model, (c) the US Delaware-Chesapeake spatially oriented model, (d) the New Zealand spatially oriented model, (e) the spawner per recruit model and (f) the life cycle model of larval allocation

Itakura et al., 2020; Machut et al., 2007). However, decreased upstream densities do not prove passage impairment because dams increase upstream habitat, which allows eels to spread over a larger area, decreasing their density. Watercourse models of eel density and distribution do not consider eel use of natural and artificial lentic waterbodies (Beentjes et al., 2016; Briand et al., 2022; Hoyle, 2016; Lambert et al., 2011). Such models may provide an incomplete picture of eel watercourse dynamics.

3.3.3 | Spatially oriented eel modelling in the Delaware-Chesapeake region of the eastern US

The difficulty of achieving a robust analytic stock assessment for American eels in US Atlantic states (ASMFC, 2012, 2017) has prompted interest in alternate approaches. This, in turn, has led to the development of a pilot spatially oriented model in Delaware and Chesapeake Bays and their watersheds, a region which possesses

both major eel fisheries and extensive freshwater and marine data resources.

A spatial database of stream connectivity and environmental parameters was assembled from the National Hydrography Dataset, StreamCat, the National Wetlands Inventory and the Freshwater Network barrier database (Table 1). Data sources used for the prioritisation of barrier removal showed a density of 0.027 dams/km² in the Pennsylvania, Maryland and Virginia portions of the Chesapeake Bay watershed (Martin, 2019a) (Table S2). Counts of small ponds from fine-scale maps (Fleming & Stubbs, 2012) and the assumption that two-thirds of ponds were formed by dams (Renwick, 2017) produced a density of 0.345 dams/km² for these states. This density is 12.5x higher than the density estimated by Martin (2019a). The difference in these density estimates implies that most small dams in the region were not included in barrier databases. For saline waters, the spatial database includes tidal and fetch mapping and bathymetry from a seamless topobathymetric elevation model (CoNED, Table 1). Most eel presence/absence, abundance and biological data are from electrofishing in streams and trawling in marine waters (Figure 5c). Modelling aims to establish landscape-scale predictive relations between environmental drivers and eel distributions and population characteristics. This task is particularly complex in fresh water because eels present at a particular location depend on site characteristics, river connectivity chains and the history of barriers in the system.

Machine learning approaches, including random forest and boosted regression trees (Breiman, 2001; Elith et al., 2008; Plant et al., 2021), accommodate the complexity of relations between eel distribution and habitat attributes, with minimal requirements for distributional profiles of predictive variables. However, the reliability of extrapolating model outcomes beyond the training range is uncertain. Random forest modelling is being examined as a tool to predict eel distribution in the Chesapeake Bay and Delaware River watersheds on the basis of watershed characteristics and to contrast distributional patterns in easily accessible downstream reaches and upstream reaches where access is more restricted. Explorations are also underway of hurdle Generalized Additive Models (hGAMs, also known as delta models), so-called because they specify a "hurdle" that a variable must overcome to attain a non-zero value. hGAMs deal with data overdispersion and zero-inflation, common issues in survey data sets, by treating presence-absence and abundance separately (Laman et al., 2018). Boosted hGAM Location, Scale and Shape models (Smith et al., 2019) offer additional power to treat complex survey data by separately modelling means and dispersion and by integrating processes of covariate selection and determination of functional forms (e.g. linear vs. non-linear).

3.3.4 | Spatially oriented eel modelling in New Zealand

The endemic New Zealand (NZ) longfin eel supports important commercial, customary (indigenous) and recreational fisheries and shares

the high diversity of life histories and habitats found in Atlantic eels, within a smaller stock area. Developing an analytic stock assessment for this population was not considered feasible due to its fractal, highly fragmented and unmixed population structure, high variability of population parameters between locations, and the fact that fished and unfished areas have different average population parameters (sex ratio, density and growth rates) (Dekker, 2000; Hoyle, 2016). A more achievable objective was to develop a spatially oriented modelling approach for long-term monitoring of distribution and trends in the overall population and in female spawning biomass.

To help guide longfin eel conservation and management, a modelling framework was founded on a digital network of 600,000 stream segments (Snelder & Biggs, 2002), with associated data on fish abundance, habitat characteristics and locations of dams (Crow, 2017). Previous modelling efforts, based on machine learning methods, were static in time (Crow et al., 2014; Elith et al., 2008). Here, an R program called Vector Autoregressive Spatio-Temporal (VAST) was introduced to treat both spatial and temporal variations simultaneously (Thorson & Barnett, 2017). VAST uses delta-generalised linear mixed modelling (delta-GLMM) to estimate spatial response variation from location-specific encounter, count and biomass data. Stream characteristics are spatially autocorrelated according to along-stream, rather than by straight-line distance. To adapt VAST to streams, a module was added to model autocorrelation using the Ornstein-Uhlenbeck process (Hocking et al., 2018). By modelling probabilities of occurrence and positive catch rates separately (Thorson, 2019), VAST estimates longfin eel density across space and time.

The first application of the model was to estimate spatial and temporal changes in the probability of encountering longfin eels in the Waitaki catchment, South Island, from 1960 to 2019. A second application modelled the density and covariation of small and large eels in the greater Waikato region over the same period. A simulation experiment used the density model as an operating model to evaluate alternative sampling scenarios for their ability to identify trends in numbers of eels larger than 50cm as a proxy for female spawning biomass (Hoyle et al., 2021).

Advantages of this spatio-temporal modelling approach include the ability to provide a time series of predictions across space, based on patterns in the data and correlations amongst samples given their proximity in a stream network or in time, and relationships with habitat covariates. The model can also integrate information from multiple data types, including occurrence, counts, categories such as size, sex or species, multiple sampling methods, and habitat and sampling covariates.

The NZ approach parallels aspects of the SUDOANG eel programme of Southwestern Europe (Briand et al., 2022), which also quantitatively links eel abundance to habitat quality, quantity, location and escapement. As with SUDOANG, the NZ approach emphasises eels in riverine habitat. Longfin eel use of lake/pond and bay/estuary habitat (Jellyman et al., 1997; Stuart et al., 2019) is not considered due to the paucity of suitable abundance measures (Charsley, 2019; Figure 5b).

3.4 | Population modelling

3.4.1 | Context

The anguillid eel life cycle alternates between oceanic and continental waters, where eels may occupy bay/estuary, riverine and lake/pond habitat (Figure 5). Population modelling aims to provide quantitative insights into eel population status and its determinants in the course of the life cycle. Population models are particularly useful if they produce BRPs against which conservation success is gauged (FAO, 1995).

Population modelling for anguillid eels is challenged by the heterogeneity of demographic parameters and mortality factors over vast species ranges and across habitats, sexes, and morphological and physiological types. The most concerted modelling attempts have been for the European eel, where the European Union (EU) has directed member states to establish management plans founded on a BRP of at least 40% of silver eel biomass relative to escapement under pristine conditions (EU, 2007). However, determining the baseline pristine condition is problematic given long histories of eel exploitation and aquatic habitat alteration (Aalto et al., 2016; Orton et al., 2017). In addition, data sets are centred on European streams and rivers and overlook production from bays/estuaries, lakes/ponds and North Africa (Basic et al., 2019; ICES, 2020a). For the American eel, a Depletion-Based Stock Reduction Analysis was used to evaluate the impact of a single factor (fisheries) in US Atlantic waters (ASMFC, 2012; Dick & MacCall, 2011). However, modelling was not judged sufficiently credible to guide management advice (Limburg et al., 2012). In the absence of robust analytic assessments, management advice for both Atlantic eel species is largely based on glass eel/elver and yellow eel abundance indices (ASMFC, 2017; DFO, 2014; ICES, 2021a).

This section outlines modelling approaches that focus on one life stage (glass eel model), trace survivorship through the continental phase (spawner per recruit model) or examine larval allocation to rearing areas (life cycle model). Comparisons emphasise the degree to which modelling approaches cover the main habitat types occupied by continental-phase eels (Figure 5).

3.4.2 | Geographically nested modelling of glass eel recruitment

Incoming glass eels and elvers represent oceanic recruitment prior to anthropogenic impacts that reduce yellow and silver eel populations. Measures of this recruitment are used as trend indicators for both Atlantic eel species (ASMFC, 2012; DFO, 2014; ICES, 2021b). However, recruitment trends vary amongst sites, and differences in gear type and placement may impair inter-series comparability. For these reasons, coast-wide indices may not reliably reflect overall abundance changes (ASMFC, 2017). This section describes the Glass Eel Recruitment Estimation Model

(GEREM), which integrates abundance indices at nested spatial scales, potentially up to the species range (Bornarel et al., 2018; Drouineau et al., 2016).

The first nested scale of GEREM is the quantity of recruits to a river's watershed, derived from fisheries-dependent or fisheries-independent data. Recruitment numbers from monitored watersheds are extrapolated to nearby unmonitored watersheds by applying a power function of watershed surface area, under the assumption that watershed attractivity is related to water discharge (Burgers et al., 2014). Recruitment numbers are summed for zones that consist of geographic clusters of watersheds, and zonal recruitments are summed across the study area. In this way, total eel recruitment has been estimated over a large part of the European eel range, although not including the Baltic Sea and the southern and eastern Mediterranean where local recruitment series and estimates of absolute recruitment are unavailable (Bornarel et al., 2018; ICES, 2020a). Also excluded are most eels that occupy bay and estuary growth habitats, owing to the location of glass eel monitoring stations at or near the heads of estuaries (Harrison et al., 2014, Figure 5a). GEREM's integrated recruitment series improve understanding of stock trends, highlight data needs and trend differences amongst regions, and serve as input for broader analyses, notably of riverine eel density and habitat use (Briand et al., 2022; ICES, 2020a).

Because glass eel/elver recruitment may be monitored at only one location per zone and because GEREM enables trend integration across zones, expansion of recruitment monitoring may be an attractive option to cover the large portion of the American eel range where abundance indicators are currently unavailable (Figure 1). However, GEREM works primarily with absolute recruitment, which is available for a single Canadian recruitment series (East River Chester, Nova Scotia) but not for the 23 US series for which only relative abundance is available (Figure 1). In some cases, modelling techniques or commercial catch data with additional assumptions may provide suitable proxies for GEREM input (Bru et al., 2009; Lin & Jessop, 2020). The reliability of water discharge as an attraction proxy is uncertain. Although the southern Gulf of St. Lawrence supports large yellow eel fisheries (Cairns, 2020), plankton surveys and repeated monitoring have caught few glass eels and elvers (Dutil et al., 2009; D. Cairns, unpublished data). Therefore, viable recruitment series may be difficult to establish in this region. The limited ability of glass eel/elver monitoring methods to measure recruitment to bays and estuaries (Walmsley et al., 2018) also means that GEREM analysis is constrained to eels destined for freshwater growth habitats.

3.4.3 | Spawner per recruit modelling

Spawner per recruit (SPR) models compare spawning production (numbers or biomass of spawning adults; numbers or biomass of eggs) per recruiting individual under scenarios with and without anthropogenic mortality (Mace & Sissenwine, 1993). SPR models can be used to set BRPs as the anthropogenic mortality that would

maintain spawning production at a given percentage of the SPR that would occur in the absence of anthropogenic effects. ICES (2001) advocated the implementation of SPR modelling for American eels with 30% limit and 50% precautionary approach BRPs of SPR in scenarios without anthropogenic mortality, values derived from typical life history characteristics of exploited fish populations (Clark, 1991). SPR has been applied to yellow and silver eel fisheries in Chesapeake Bay estuaries (Fenske et al., 2011; Weeder & Uphoff, 2009), hydroelectric turbine mortality in a Chesapeake tributary (Sweka et al., 2014), and glass eel fisheries and turbine mortality in Nova Scotia (DFO, 2019). SPR can also treat populations that have variable life histories, multiple forms of anthropogenic mortality, and cumulative impacts by modelling population segments separately and then summing their spawner production outcomes (Chaput & Cairns, 2011).

A full implementation of SPR to the American eel in a particular watercourse would require estimates of arriving glass eels and annual tracking of major demographic parameters (sex-specific weight, growth rate, maturation probability, natural and anthropogenic mortality, population biomass) until the cohort has fully departed for the spawning area. However, if anthropogenic mortality occurs only during a specific episode of the eel's continental life, SPR models can be applied to these episodes by treating cohorts before the mortality event as "recruits" and after the mortality event as "spawners." SPR-based BRPs have been calculated in this way for glass eel fisheries and silver eel turbine mortality in Nova Scotia (DFO, 2019).

Spawner per recruit is an attractive modelling option for American eels because many input data are known or can be approximated from the literature. However, some aspects of the theory underlying SPR align poorly with American eel circumstances. SPR-based BRPs draw from the interlocking concepts of stock-recruitment (SR) relationships and maximum sustainable yield, in which a stock, diminished from its carrying capacity by fishing or other anthropogenic pressure, responds with a productivity increase that is a non-linear function of population size (Russell & Potter, 2003; Zhou et al., 2019). The nature and existence of SR relationships in anguillid eels are uncertain, because the alternative hypothesis, that recruitment variation is dominated by environmental factors rather than by adult population size, has not been disproven (Fenske et al., 2011; ICES, 2021c). Some SPR formulations for anguillid eels call for BRPs to be set as percent reductions from the "pristine" stock biomass (ICES, 2021c), but this is challenging to implement because pristine stock biomass is difficult to estimate. Consequently, SPR modelling typically sets BRP targets and limits as a function of recruitment to the watercourse, without reference to overall stock status. This leads to counter-intuitive management guidance that some fisheries exploitation is permissible even if recruitment to the watercourse falls close to zero.

Density affects a broad range of anguillid eel demographic traits (Righton et al., 2021). For example, European glass eel survival varied 213-fold with density in a Mediterranean lagoon (Bevacqua et al., 2019). Density dependence, a core concept of SR relationships, is not considered by SPR modelling. This may lead

to unreliable conclusions, especially if anthropogenic pressure occurs at early continental stages. In a Nova Scotia river, fished only at the glass eel stage, SPR analysis of glass eel exploitation rates of 5%–65% provided estimates of anthropogenically induced spawner reductions of the same values (DFO, 2019). If early continental survival is strongly density dependent, actual anthropogenic effects on spawner production may be less because harvest removal of some glass eels would increase the survival rate of those that remain.

Given these complexities, SPR model outcomes are perhaps best seen as a first approximation of eel conservation needs for individual watercourses. A broader contribution of SPR to stock-wide status understanding requires consideration of spawner output from unexploited watercourses (Hoyle & Jellyman, 2002) and local and stock-wide density dependencies in the stock-recruitment relationship (Kapur et al., 2021).

3.4.4 | Life cycle modelling to examine eel larvae allocation effects

The American eel has long been considered a panmictic species that spawns uniquely in the Sargasso Sea and whose progeny disperses randomly across its continental range (Pujolar & Maes, 2016). This narrative may hide complexities yet to be elucidated. For the European eel, genetic analyses suggest that the overall spawning area might contain distinct zones to which female eels preferentially return, whilst genetic flow due to non-philopatric males maintains the symptoms of panmixia (Baltazar-Soares & Eizaguirre, 2016; Ragauskas et al., 2017). Female philopatry has also been proposed as a source of geographic genetic variation within the European eel's continental range (Baltazar-Soares et al., 2014). For American eels, the timing of larval detrainment from the Gulf Stream, and therefore the latitude of continental rearing destinations, could be passed between generations under a mechanism of maternal inheritance of biological clock components (Jessop & Lee, 2016).

The possibility that spawning Atlantic eels exhibit a type of philopatry below the species level has implications for conservation management. Vélez-Espino and Koops (2010) proposed the construction of a global biological model for American eels based on regional sub-models that reflect latitudinal gradients in major demographic parameters. Using a seven-zone subdivision of the east coast of North America, Young and Koops (2014) developed a stage-, age- and sex-structured life cycle matrix model, with input parameters specific to the seven zones but generalised across bay/estuary, riverine and lake/pond habitat types (Figure 5f). Model runs examined several larval distribution hypotheses: (a) full maternal attraction (larvae return exclusively to the zone where their mothers reared); (b) full water attraction (larvae are distributed amongst zones in proportion to the zone's watershed area [a proxy for water discharge]); (c) a strong maternal (0.95) with a weak water attraction and (d) a strong maternal attraction (0.95) with weak straying to adjoining zones.

Young and Koops' (2014) model outputs for full maternal attraction (a) showed zonal populations that are discrete in the matrilineal line. In this scenario, the attainment of conservation benchmarks in local zones should reliably produce both local and species-wide conservation success (distributed control approach; Dekker, 2016). However, under assumptions that larvae are incompletely or not at all maternally philopatric (b, c, d), modelling demonstrated strong and sometimes counterintuitive effects of larval interchange amongst zones, at times producing large deviations from population trajectories expected from local demographic rates. These findings suggest that conservation strategies for eels should account for both local drivers of population dynamics and dynamics of population interchange amongst zones.

4 | DISCUSSION

4.1 | Data

Traditionally, fish biologists collect data on the distribution and abundance of their species of interest. However, with only a small cadre of eel researchers and a plausible historic continental range of 8.5 million km² (Figure 1), eel-directed field collections cannot possibly meet assessment data requirements. Current public databases provide some eel records (Table 2), but no public databases systematically cover electrofishing, fishway passage or eDNA metabarcoding surveys, all of which detect eels. Data mining is an appropriate approach for obtaining data gathered by diverse methods from scattered sources (Benchetrit & McCleave, 2016), but fisheries data gathered at public expense using standard methods should be housed in public databases.

Environmental databases, key enablers of spatially oriented modelling, have large gaps in eel-relevant data. The widest of these is in dams. Most dams (~90%) in the conterminous US are not inventoried (Tables 1 and 3, Tables S1 and S2). The proportion of uninventoried dams in Canada and the Caribbean may be at least as high. Public posting of data on fish distribution and abundance, and broadening of environmental databases to include more features that impact aquatic animals (e.g. small dams), could aid the conservation of a wide range of aquatic fauna, including eels (LaDeau et al., 2017). In Europe, collaboration amongst diverse environmental stakeholders and widespread use of crowdsourcing have put needed data in the hands of eel biologists (Belletti et al., 2020; Drouineau et al., 2021). The recent development of a machine learning algorithm that uses geospatial and lidar data to identify dams, even small ones, with reasonable accuracy (true positive rate 89%, false positive rate 1.2%) (Buchanan et al., 2022) may open the door to comprehensive inventories of dams of all sizes.

Information on fish, including eel, abundance in lentic waters (bays/estuaries, lakes/ponds) is often scant. Mark-recapture surveys can measure eel abundance at high labour cost (Diekmann et al., 2019). Where technique-specific conditions (notably water

depth and clarity) are met, boat electrofishing, glass-bottom boat surveys and net enclosures may enable efficient measurement of eel abundance (Table 4). These are multi-species techniques, which opens the potential for data- and cost-sharing partnerships with specialists in other species.

eDNA is the cheapest method of field surveying because the collection of filtered water is simple and laboratory analysis is automated and efficient. Current eDNA work has two threads. Metabarcoding identifies a broad range of species (Miya, 2022), which means that general-purpose surveys can help map American eel distributions. qPCR detects eDNA of targeted species with greater sensitivity and also measures its concentration (Kasai et al., 2021). Measured eDNA concentrations can be used to predict organism abundance by calculating their relation to populations estimated by independent methods (Chin et al., 2021). The inability of eDNA concentrations to fully explain the variance of independent population estimates is attributed to factors, other than organism abundance, that affect eDNA concentrations (notably variable rates of eDNA release, degradation and dispersal) (Caza-Allard et al., 2022). However, focus on these factors overlooks the role of error and bias in independent population estimates in clouding relations between eDNA concentrations and populations (Yates, Cristescu, et al., 2021). In particular, multi-pass removal electrofishing, commonly used to estimate the abundance of stream fishes, may underestimate abundance due to a violation of the assumption of constant detectability across passes (Hedger et al., 2018; van Poorten et al., 2017). Robust correction factors to convert eDNA concentrations to abundance, and measurements of the error of the method, could be obtained by releasing known numbers of eels in closed natural waters and then, after an acclimatisation period, comparing measured eDNA concentrations to known population sizes (see Harris et al., 2016; Stewart et al., 2019). Inclusion of other abundance estimation techniques (mark-recapture, electrofishing, glass-bottom boat surveys, net enclosures; Table 4) in such experiments would provide comparisons of method accuracy that would help eel researchers choose the best methods for their work.

Given their high labour requirements, there is no foreseeable prospect that non-eDNA survey methods will map American eel distribution and estimate its abundance over the species' vast plausible range, especially in the Southern Zone where fisheries monitoring infrastructure is limited. Facilitated by its low cost, the eDNA technique has a chance to attain broad coverage for distribution, and possibly also for abundance. Technical advances that combine the broadband application of metabarcoding and the sensitivity of qPCR (Boivin-Delisle et al., 2021; Hoshino et al., 2021) may assist.

In contrast to all other American eel abundance series, oceanic larval tows furnish an abundance series that represents the entire stock. The three currently available data points (Figure 3) will be extended by three additional points not yet published and by the planned continuation of eel-centred research cruises to the Sargasso Sea spawning area (R. Hanel, personal communication).



Data on demographic parameters generally require species-specific studies. Spatial analysis takes advantage of the tendency of demographic parameters to vary with environmental factors, which enables the estimation of parameters where local field data are absent (Gruss et al., 2021). Age data are crucial to many types of population analysis. Age estimation by the DNA methylation technique has been validated for an expanding number of fish species (Weber et al., 2022), and its application to American eels could increase the supply of age estimates at low cost whilst avoiding lethal sampling.

4.2 | Habitat

Selection of growth habitat (bays, estuaries, rivers, streams, lakes and ponds) by recruiting American eels (Figure 5) has consequences for growth rate, likelihood of becoming male or female and time to maturity (Cairns et al., 2009; Vélez-Espino & Koops, 2010). For eels recruiting to fresh water, the journey to and from habitat destinations often involves additional obstacles and risks (Woods & McGarvey, 2018). For these reasons, eel population dynamics and use of space are inextricably linked.

Herein, we propose approaches to eel habitat modelling that may have broad potential. First, we revisit the long-standing assumption that all impacts of dams on eels are negative. Negative effects on eels are expected for medium and large dams that strongly or fully block upstream passage and because many possess turbines that often kill downstream migrants (Mensingher et al., 2021). Small dams rarely contain turbines and more likely permit eel passage (Lamson et al., 2006). For small dams, a simple conceptual model showed that eel densities above a dam will decline even if upstream passage is unimpaired because the same number of eels will be spread across a habitat whose area is increased by impoundment formation (Figure 4). Modelled scenarios are supported by observations of similar eel densities above and below small dams and evidence of bi-directional traffic across them.

Small ponds, numerous and widespread around the world (Lehner et al., 2011) and capable of supporting high eel densities (Stewart et al., 2021; Table S5), clearly affect anguillid conservation. Small dams both create habitat and disrupt access to it. However, small ponds and dams are largely overlooked in eel status assessment. Ponds are not considered in population models of the New Zealand longfin eel (Hoyle, 2016) and of the European eel in Southwestern Europe (Briand et al., 2022). Models of eel watercourse colonisation assume that all density depression above dams are caused by passage impairment (Beentjes et al., 2016; Briand et al., 2022; Hoyle, 2016; Lambert et al., 2011). Campaigns to enhance watercourses by dam removals do not account for habitat reduction caused by draining of ponds (Hermoso et al., 2021; Lin et al., 2019; Martin, 2019b). An understanding of the role of small dams and ponds in eel conservation will require the expansion of dam inventories, measurements of eel abundance in impounded reaches and integration of these data into watershed-scale modelling of eel abundance and dynamics (e.g. EDA; Briand et al., 2022).

Eel modelling in impounded watercourses must also consider downstream passage. Telemetry studies in watercourses with small turbine-free dams show that down-migrating silver eels often slow and even stop. Persistent exploratory behaviour within impoundments is interpreted as evidence that these interruptions are due to suppression in lentic waters of flow cues that both trigger and guide migration (Drouineau et al., 2017; Mensinger et al., 2021; Trancart et al., 2018, 2020). However, delays and halts in silver eel down migration also commonly occur in undammed rivers (Béguer-Pon et al., 2014; Stein et al., 2016). In addition, otolith microchemistry suggests bi-directional traffic across dams that separate head-of-tide impoundments from adjacent estuaries (Lamson et al., 2006). Large reservoirs, up to 100s of km long, have been characterised as hostile environments for migratory fish, heightening predation risk and blocking downstream migration through suppression of current-based orientation cues (Pelicice et al., 2015). In contrast, the two largest lakes in the American eel range, Lake Ontario (300km long) and Lake Champlain (120km long), formerly supported abundant populations of yellow eels that produced large runs of escaping silver eels (LaBar & Facey, 1983; Mathers & Stewart, 2009; Verdon et al., 2003). Watercourses consisting of the river-lake chains, which are especially common in the glaciated northern portion of the American eel range (e.g. figure 1 of Jessop et al., 2002), mimic the lentic-lotic alternation of impounded systems. Comparative investigations of silver eel migratory dynamics in natural and artificial lentic-lotic systems may shed light on how down-migrating eels address the challenge of finding small outlets to large bodies of standing water.

A second spatially oriented approach is to model relations between populations and environmental factors. Advances in modelling techniques, including those based on machine learning (Laman et al., 2018; Smith et al., 2019), allow a multiplicity of demographic and environmental variables of diverse form and type (e.g. binary, eel encounter vs. non-encounter; continuous, eel density) to be examined in a single framework. These techniques have been applied to the American eel in the Delaware-Chesapeake region of the US and to longfin eels in New Zealand (Figure 5c,d). For the longfin eel, the R program VAST has added temporal capability to spatially oriented modelling, with the prospect of offering robust regional time series of spawner production and quantification of demographic responses to environmental drivers (Hoyle et al., 2021). For the European eel, spatially oriented modelling has produced escapement estimates in some subpopulations (Briand et al., 2022; European Commission, 2020), and a recent review recommended spatially oriented modelling as a central pillar of future assessments (ICES, 2021c).

Spatially oriented modelling is most useful when it embraces eels from all habitat types. Current spatial modelling work on American, longfin and European eels largely focuses on stream electrofishing as a data source for occurrence and density (Figure 5b-d). Application of novel and underutilised survey techniques for lentic waters (Table 4) may yield data that facilitate the expansion of spatially oriented modelling to eels occupying bays, estuaries, lakes and ponds.

4.3 | Towards a range-wide stock assessment

In their basic form, analytic stock assessments assume a well-mixed pool of animals without spatial heterogeneity (Kapur et al., 2021). In contrast, Vélez-Espino and Koops (2010) proposed that spatial variability in American eels could be modelled by creating regional sub-pools, with demographic traits estimated from temperature and latitudinal clines. In such an arrangement, range-wide outputs (e.g. for spawner biomass) would be the sum of regional sub-pool outputs. This approach echoes the system mandated by the European Union for the European eel, in which findings for geographic sub-units (river basins or collections of river basins) are tallied across the EU territory (EU, 2007). However, intense demographic variation at scales below regions and river basins arises notably from habitat selection, sex, intragenerational genetic shifts and differential anthropogenic pressures (Babin et al., 2017; Cairns et al., 2009; Jessop, 2010). In theory, these sources of variation could be modelled by splitting pools into smaller and smaller units, until within-pool heterogeneity disappears. However, for the New Zealand longfin eel, Hoyle (2016) argued that pools small enough to be well mixed would be too numerous to characterise or model, and that geographic fragmentation further obstructs the reliable measurement of demographic traits. Consequently, analytic assessments are impractical to achieve. Hoyle (2016) instead advocated spatio-temporal modelling, which promises less (it does not estimate BRPs), but has a better chance of attaining intended end points (e.g. time series of spawner production).

The ideas and resources outlined herein may help build scientific capacity for both analytic assessments and spatio-temporal models. Data mining will bring to light useful information on American eel distribution and abundance, but the creation of new data, especially by eDNA, is required to define eel occupancy across its enormous plausible range. Spatial analysis methods could be a knowledge multiplier for eels, if relationships established in a study area can be used to estimate population and habitat use attributes in larger outside territories. However, gaps in environmental databases (notably non-coverage of small dams) constrain this potential. Bay/estuary, lake and especially small pond, habitat is underserved in anguillid eel status evaluations (Briand et al., 2022; ICES, 2009; Figure 5). Modelling that recognises density dilution by impoundment formation (Figure 4) can help clarify the effects of small dams on eels, but data on eel abundance in ponds, needed to implement this approach, are scant (but see Table S5). The GEREM glass eel model can integrate local recruitment series potentially range wide, but only one available time series (East River Chester, Nova Scotia; Figure 1) provides the absolute recruit numbers that the model requires. SPR models can be implemented with available data or reasonable proxies in some Atlantic Zone locations, but SPR does not recognise stock-level considerations, such as the imperative to stop fisheries and other anthropogenic mortality if the species population is low.

Findings from regional modelling, whether analytic or spatially oriented, should produce absolute (rather than relative) eel abundances, so that their sums will accurately reflect range-wide totals

(Hoyle & Jellyman, 2002). Field methods that measure absolute (or at least minimum) eel abundances may help address this need (Table 4). The planned extension of oceanic larval surveys could lead to an eel abundance time series that is exempt from spatially varying continental effects. In conjunction with continental recruitment data, this series may also shed light on the role of larval survival in American eel population dynamics. Insights into the ocean survival of adult migrants are less likely because escapement time series are available from only a single watercourse (the St. Lawrence River, Figure 1). Despite a century of ocean research (Miller et al., 2015), the paradigm of random larval dispersion from the Sargasso Sea spawning area is neither proven nor disproven (Baltazar-Soares & Eizaguirre, 2016; Jessop & Lee, 2016). The life cycle model of larval allocation (Figure 5f) offers a platform to explore deviations from random dispersion, which has significant implications for American eel conservation and stock assessment design.

The ideas presented herein address only a small portion of the assessment challenges that face American and other anguillid eels (Righton et al., 2021). Expectations that a road map towards American eel stock assessment can be implemented, or even formulated, in the near future must be tempered by the reality of what we do not yet know. Spatial modelling may be an alternative to (Hoyle, 2016) or a partner with (ICES, 2021c) conventional analytic techniques. Determining the relative roles of these approaches, a crucial step, will help guide the collection of data needed to represent the vast understudied reaches of the species range. In addition, better channels are required to widely share both extant and new data sources. By drawing ideas from within (e.g. glass-bottom boat surveys) and outside (e.g. net enclosures, the glass eel model) the American eel range, this article emphasises worldwide collaboration as a key enabler of progress. We anticipate that the recently announced ICES Working Group on American Eel (prep.ices.dk/about-ICES/Documents/Resolutions/2021%20Resolutions/FRSG%20Resolutions%202021.pdf) will play a central role in marshalling data, weighing options and charting courses towards stock assessment goals.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Sources of datasets described in this paper are given in tables and figures of the main article and its Supporting Information.

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