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## Methods and data sources to support American eel population analysis

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## Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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## ABSTRACT

The American eel (*Anguilla rostrata*) occupies a vast range in the West Atlantic Ocean and inflowing waters. Despite its presumed panmictic status, management of this species is geographically fragmented. There have been widespread calls for internationally coordinated efforts towards a range-wide stock assessment, but such an objective faces obstacles of a high degree of heterogeneity in major life history characteristics and the near-absence of such data in the northern, western, and southern parts of the species' range. This paper reviews novel and underutilized methods and data sources that may aid progress to an eventual range-wide assessment. Methods for obtaining information on distribution and abundance include mining of extant data and field surveys by glass bottom boat, electrofishing boat, net enclosures, environmental DNA (eDNA) and ocean larval tows. Analytic resources and tools include environmental databases, fetch as a covariate of abundance, accounting for the net effects of small ponds, GIS-oriented habitat modeling, glass eel-oriented population modeling, estimation of age structure from length structure, use of life history parameter clines to fill gaps in assessment input values, and life cycle modeling. eDNA is a cost-effective technique that has the potential to clarify American eel distribution, and possibly relative abundance, over the very large areas where data for this species are sparse. Most other techniques reviewed in this paper have substantial costs, which may constrain their use in the southern part of the American eel range where resources of aquatic science are often limited.

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## INTRODUCTION

The American eel (*Anguilla rostrata*) occupies a vast area of the West Atlantic Ocean and adjacent waters, with a continental range extending from Greenland to northern South America. American eels attract public interest because of their mysterious life history and have a high cultural significance among indigenous peoples. American eels are subject to commercial fisheries in some parts of their range and their glass eel stage contributes seedstock to the east Asian *Anguilla* eel aquaculture industry, which is worth billions annually. American eels have been assessed as threatened in Canada (COSEWIC 2012), depleted in US waters between Maine and Florida (ASMFC 2017), not in any category in the United States (US Department of the Interior 2015), and endangered internationally (Jacoby et al. 2014).

Genetic sampling of American eels between Newfoundland and Atlantic Florida and from the Northeastern Gulf of Mexico shows an absence of geographic structure in neutral genetic markers (Gagnaire et al. 2012, Côté et al. 2013, Bonvechio et al. 2018). These findings have been interpreted as indicating that the American eel comprises a single panmictic stock, although genetic analyses are unavailable from the northern, western, and southern part of the species range. For the closely related European eel (*Anguilla anguilla*), panmixia has been confirmed through a sampling program conducted on leptocephali in the Sargasso Sea spawning site (Als et al. 2011).

Despite the American eel's presumed panmictic status, its management is geographically fragmented. Fisheries management and conservation oversight, where they occur, are organized nationally or subnationally. Population assessments are conducted in subsets of the species range, or (in most areas) not conducted at all. Presumed panmixia is the main impetus for repeated calls for international collaboration leading to a range-wide stock assessment (Loftus 1982, Ritter et al. 1997, ICES 2001, DFO 2010, Velez-Espino and Koops 2010, ASMFC 2012, Limburg et al. 2012, DFO 2014).

In Canada, American eel status has been subject to three major reviews in the 2010s (DFO 2010, COSEWIC 2012, DFO 2014). The latter exercise, mandated as a Recovery Potential Assessment under the Species at Risk Act (SARA), provided detailed examinations of eel habitat needs, threats, population trends, and prospects for reversal of population declines (Cairns et al. 2014, Chaput et al. 2014, Pratt et al. 2014). In Canada there is an ongoing need for robust eel conservation advice, arising from issues in determining sustainable fisheries harvest, designation under SARA, and evaluations under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). These pressures, coupled with consciousness of the need to examine American eel status through a wider geographic lens, led to two workshops held under the auspices of DFO Science Branch's Canadian Science Advisory Secretariat (CSAS). These workshops were jointly titled "Stock-wide Assessment Framework for American eel." The first workshop (Part 1- Review of available data), held on 15-16 May 2019 in Ottawa, compiled available data on landings and abundance series and reviewed the methodology and potential errors and biases that might affect the quality of abundance indicators (Cairns 2020). A second workshop, held on 29-31 October 2019 in Halifax (Part 2- Review of trends and approaches to assessment) reviewed abundance trends and approaches to assessment. The present paper was a contribution to this second workshop.

This paper contributes to the mandate of the second CSAS workshop by outlining novel and underutilized methods and data sources that could potentially aid progress toward a range-wide American eel stock assessment. It is based on the premise that the scope and difficulty of a range-wide assessment is such that new ways of doing business are required. The paper outlines the potential and limitations of these ideas but does not attempt a definitive evaluation

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of their scientific or practical viability. Instead, it aims to encourage and facilitate the examination and testing of new approaches. It will be up to future researcher to determine, which, if any, approaches presented in this paper are capable of contributing toward a range-wide American eel stock assessment.

## **CHALLENGES TO A RANGE-WIDE AMERICAN EEL ASSESSMENT**

Fisheries stock assessment science is a long-established discipline that draws on a large body of biological knowledge and analytical toolsets. Most stock assessments are conducted on fish stocks whose range is a fairly small fraction of a whole ocean, within which habitat, life history patterns, and demographic traits are broadly similar. With most assessed stocks, all members of the stock are at risk of exploitation during at least some part of their life cycle, and exploitation is sufficiently intense to have an effect on population size and population dynamics. If suitable monitoring data are available, it is possible to assess status of such stocks with age-structured tools such as virtual population analysis and statistical catch at age models. If less than a full suite of monitoring data are available, the stock can be assessed with surplus production models or with one of the burgeoning list of data-limited assessment techniques (e.g. Carruthers et al. 2016, Wiedenmann et al. 2019).

In contrast to typical assessed stocks, the American eel's range extends throughout the western part of the North Atlantic Ocean from sub-polar to tropical waters over a north-south distance of 7,000 km (Fig. 1). It also extends about 5,000 km on the east-west axis, from deep ocean to mountain slopes, over a huge continental area in North, Central, and South America. Within this range the American eel traits exhibit a high degree of geographic heterogeneity, a pattern that Dekker (2000) termed (for the European eel) fractal geometry. American eels collectively experience a very broad range of temperatures, which in turn is linked to large variation in many biological functions (Jessop 2010, Velez-Espino and Koops 2010). American eels occupy both fresh and salt water, exhibiting marked growth differences between these habitats (Cairns et al. 2009). Male and female eels mature at different schedules, causing further variation in demographic traits (Jessop 2010). American eel status as a single genetic stock in eastern North America (Gagnaire et al. 2012, Côté et al. 2013, Bonvechio et al. 2018), and presumed panmictic status for the entire species, imply that eel abundance indicators should track a common underlying population trend, allowing for sampling error and with variations due to local effects. However, measured abundance trends vary widely among sampling sites (Cairns 2020). The American eel is commercially fished, but unlike most assessed fish stocks, fishing is concentrated in limited areas (Fig. 1), leaving eels in the majority of the species' range unexposed to exploitation.

A further complexity of eel biology is that despite presumed panmixia, eels exist as different ecotypes with different growth rates, sizes and sex ratios according to recruitment location (Côté et al. 2015, Pavey et al. 2015, Drouineau et al. 2018). Pavey et al. (2015) found that ecotypic differences between eels occupying different habitats is not solely due to phenotypic plasticity, but may also arise from functional genetic differences stemming from either or both intra-generational spatially varying selection and genotype-dependent habitat choice of ecologically divergent habitats. An individual-based optimization model further explores the roles of adaptive phenotypic plasticity and genetic-dependent habitat selection (Mateo et al. 2017).

Any American eel assessment at the scale of the entire species needs to account for spatially varying abundance trends. Eel recruitment and abundance in the upper St. Lawrence River and Lake Ontario (outer portion of the range) have declined by something like two orders of magnitude in the last 35 years (Castonguay et al. 1994, Dekker and Casselman 2014). In contrast, St. Lawrence silver eel indices, which reflect status and productivity for the entire St.



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Lawrence Basin, have declined by about two thirds. Elsewhere in Canada, no locations show declines as steep as those of the upper St. Lawrence (Cairns 2020). Drouineau et al. (2018) argued that hydro dams and fishing have exerted high selective mortality on St. Lawrence River eels for 30 years or more (ca. two eel generations in fresh water), which in turn reduced the prevalence of eel ecotypes adapted to such habitats (longest migration, most distant areas from the spawning site). If correct, this hypothesis may explain why recruitment to the upper St. Lawrence River has declined drastically in contrast to the remainder of the species' range despite presumed panmixia.

In typical assessed fish stocks, monitoring series that are maintained over time and are distributed across the stock range adequately represent the stock's main features. For the American eel, nearly all biological and demographic data come from the Western Atlantic region (Figs. 1-3). Outside this region, which is the majority of the species range, demographic data are unavailable and habitat occupancy and range limits are only sketchily known (local exceptions include Texas (Hendrickson 2017), Costa Rica (McIarney 2017), and Puerto Rico (Kwak et al. 2019)). This means that no set of demographic data reliably represents the American eel across its range.

Because of wide geographic variation in demographic traits and the uneven distribution of fishing pressure, the American eel cannot be readily assessed by the age-structured and data-limited methods noted above, even if range-wide demographic data were available. Assessment approaches that embrace geographic variation in demographic traits have been applied to two *Anguilla* species. The European eel has a large continental range in Europe, northern Africa, and west Asia, over which demographic traits vary widely. The European Union has developed a management approach based on Eel Management Units, which are small enough to contain eels with relatively similar demographic traits. Assessments aim to determine compliance with the objective of silver eel escapement attaining or exceeding 40% of that which would occur in the absence of anthropogenic impacts (EU 2007, ICES 2018). A similar approach has been applied to the segment of the American eel range that falls within Maritimes Region in eastern Canada (DFO 2019a). In New Zealand, GIS methods have been applied to the endemic longfin eel (*Anguilla dieffenbachii*) to develop habitat classifications and habitat-specific abundance estimates (Beentjes et al. 2016, Hoyle 2016).

The European eel has been subject to long-standing multi-national assessment efforts (ICES 2019). The European eel is better studied than the American eel (a Web of Science search for 1955-2018 shows that papers that include "*Anguilla anguilla*" (N=4,264) are 5.7 times more numerous than papers that include "*Anguilla rostrata*" (N=751)). Despite international collaboration and a larger information base, the European eel assessment falls short of full coverage of the stock. Coverage omits a major habitat type (coastal and estuarine growth areas) and a major geographic zone (African and Asian coasts of the Mediterranean Sea) (ICES 2009, 2018). In France, assessment work is founded on a model called Eel Density Analysis (EDA) (Anon. 2018, Briand et al. 2018). Silver eel production for some (but not all) zones not covered by EDA has been estimated by crude methods that are considered accurate only to an order of magnitude. Based on these numbers, EDA estimates of silver eel production account for only 14% of total silver eel production for France (production in number of eels) (Anon. 2018).

The most important obstacle to a range-wide American eel assessment is the absence of data on demographic traits, abundance trends, and habitat occupancy over most of the species' range. In the data-rich Western Atlantic area, the canon of eel data has been built up by decades of eel-directed studies. Progress towards a range-wide assessment requires more efficient techniques to obtain key information over wider geographic areas. It also requires

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analytic techniques that can produce valid insights in the face of data gaps that will inevitably persist.

## DISTRIBUTION AND ABUNDANCE

### MINING OF RANGE RECORDS (CONTRIBUTORS: DAVID CAIRNS, JOSÉ BENCHETRIT, LUKE POIRIER, AND TREVOR AVERY)

Data mining is the process of extracting information from large or broadly distributed information sources. Four types of data mining for American eel distribution and abundance information are described as follows.

#### **Type A. Accessing professionally maintained biodiversity databases**

There is an accelerating trend to assemble large masses of natural resource data from diverse sources into databases with regional, national, or global scopes (Ladeau et al. 2017, Isaak et al. 2017, 2018). Table 1 lists databases that show or potentially show American eel records. Databases such as Global Biodiversity Information Facility (GBIF) and Ocean Biogeographic Information System (OBIS) draw their information from credible scientific sources and may contain detailed metadata on individual records. iNaturalist accepts contributions from amateurs, but some records are subject to verification and are considered research-grade. The Aquatic eDNA Atlas, newly expanded to include the eastern US, is crowd-sourced from professional contributors. For the eastern US, IchthyMaps (Frimpong et al. 2016) compiled freshwater fish records up to the early 1990s. Although databases such as these are increasing in their scope and coverage, most survey data relevant to American eel distributions are not yet in publically accessible databases. This includes electrofishing databases maintained by federal, provincial, and state agencies. Most of the American eel continental range is not treated by any comprehensive and up-to-date database of freshwater fish records.

#### **Type B. Assembling databases of data solicited from researchers and agencies**

If a needed database does not exist, it is often possible to create one simply by asking researchers and agencies for their files. A freshwater example is Lapointe et al. (2016), who assembled a database of 75,636 fish records supplied by fisheries agencies in mid-Atlantic US states for a project on invasive fish pathways.

In saline (brackish and salt) water, multi-species surveys, using non-selective gear, are commonly used by fisheries agencies to monitor the distribution, abundance, and biological characteristics of marine biota. Cairns et al. (2017) assembled a database from 26 trawl and beach seine survey datasets from government, academic, and private sector sources. The database spanned waters between Hudson Strait and Florida and the years 1959-2013 and included 248,769 set records. Plots of these points represent the first time that the marine growth-phase distribution of any *Anguilla* species has been mapped at a continental scale (Fig. 4). Table 2 and Fig. 4 show 44 additional surveys, potentially capable of indicating eel distribution, that have not been brought into any multi-survey database. Some of these surveys have been evaluated for use as abundance indicators in US assessment work (ASMFC 2017) but rejected because of low eel encounter rates. However, in animal distribution studies, the determination of the range limit is always an objective, so a survey may be useful even if it shows low or nil encounter rates.

Analysis in Cairns et al. (2017) demonstrates uses to which a multisurvey database can be put. The relative importance of fresh, brackish, and salt habitats to eels is poorly known. Surveys in multiple river-estuary axes (e.g. Hudson, Delaware, James) allow replicated examinations of

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patterns of eel abundance variation along salinity gradients (Figs. 4 and 5; data from Kahnle and Hattala 2010, USFWS 2013, PSEG 2009 and 2013, and Tuckey and Fabrizio 2009). Within estuaries, relative abundance tends to peak near the limit of salt penetration, and falls away in the salt water of large bays.

The wide spatial coverage of the 70 compiled and not yet compiled surveys noted above raises the prospect of a geographically comprehensive quantitative habitat model for growth-phase American eels on North America's east coast. The key issue in such an enterprise is comparability among surveys. Cairns et al. (2017) converted trawl and seine catch rates to numbers of eels caught per unit of swept area. However, eel catchability for the various gears is unknown and probably low, so there is no "common currency" for inter-conversion of relative abundance among surveys.

### **Type C. Searching for individual and dispersed records**

Benchetrit and McCleave (2016) were the first (and still only) researchers to systematically examine American eel distribution in the wider Caribbean region (e.g. Fig. 6). In Latin America and the wider Caribbean, fisheries agencies are often of recent origin and have limited resources to comprehensively monitor marine biota. Benchetrit and McCleave (2016) started their work by searching international databases (GBIF, OBIS, FishBase) for records of preserved American eel specimens. Such records may include collection location and date, collector name, and the institution where the specimen is housed. Large institutions (e.g. American Natural History Museum, Canadian Museum of Nature), have online databases that give direct access to specimen data. In smaller institutions (e.g. the Zoology Museum of the University of Costa Rica), it was necessary to contact museum curators for information on number of specimens per record, details on capture location and other relevant information. In two instances, one of the authors visited collections (Ottawa, Mexico City) opportunistically to inspect American eel records. The author was able to visually identify one of these (in Mexico City) to be of a non-anguillid eel misidentified as an American eel.

Following the general approaches of Matamoros et al. (2015) and Tedesco et al. (2017), Benchetrit and McCleave (2016) mined primary and grey literature, including such documents as historic and recent fish checklists. Positive records were followed up with author or agency contacts to obtain additional information and clarity. These searches also documented sources with an absence of eel records, which are necessary to establish distributional limits (Elith and Leathwick 2009). Such an approach permitted the authors to map the American eel's probable southern limits in northern South America.

Huang and Frimpong (2015) discuss common pitfalls of using museum records to map freshwater fish distributions. These include unreliable capture locations that were collected before the era of GPS and occurrence records in insufficient numbers to delineate range edges. Benchetrit and McCleave (2016) dealt with these issues by assessing each record against ancillary information (e.g. capture location, date, collection technique) that inform a reliability judgement. Regardless of these biases and challenges, data mining as adopted by Benchetrit and McCleave (2016) was the only practical approach to expand knowledge of American eel distribution in the wider Caribbean.

### **Type D. Mining historic landings reports**

Historical accounts of early American usage emphasize general high abundance (MacGregor et al. 2009) but do not systematically report fine-scale presence or abundance indicators over large geographic areas. Beginning in 1867, the Canadian Department of Marine and Fisheries began recording American eel landings ([publications.gc.ca](http://publications.gc.ca)). In subsequent years, reporting of

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eel landings spread to all Canadian jurisdictions, and became geographically specific to the level of county and community within counties. These departmental reports also provide detailed narratives of fishing activities and conditions, including those for American eels. Fig. 7 shows community-by-community eel landings for Halifax County, Nova Scotia, for 1876.

Absence of landings do not prove absence of eels, but presence of landings, especially those sustained over years, proves eel presence. These historic documents may help define the minimum American eel range in the late 19th century and early 20th century along Canadian coastlines and major waterways (e.g. St. Lawrence River). In the US, eel landings were reported in annual [Reports and Bulletins of the US Fish Commission](#) starting in 1879. In some years and areas these reports also gave geographically specific data, which may help define minimum range.

### **ABUNDANCE FROM GLASS BOTTOM BOAT SURVEYS (CONTRIBUTOR: DAVID CAIRNS)**

American eel densities are useful because they can be used to calculate population size if habitat area is also known. Estimates of population size open doors to many types of analysis and modeling. Many American eel density estimates have been generated for freshwater streams by electrofishing surveys (Cairns et al. 2007, Cairns 2020). Far fewer density estimates are available for lentic (non-flowing) habitats (see compilation in Cairns 2020). The main traditional method to estimate eel densities in lentic habitats is Capture-Mark-Recapture (CMR).

Cairns et al. (2009) and Hallett (2013) developed a method to estimate American eel densities from nighttime glass bottom boat (GBB) surveys. A wooden boat, fitted with a triangular viewing window of tempered rink glass, was propelled by oar or by trolling motor across ponds, estuaries and other non-flowing waters (Fig. 8). Light was furnished by LED lamps fixed to a bow-mounted underwater shelf that also served to divert turbulent bubble-laden water away from the viewing window. A prone observer recorded eels and habitat characteristics into audio files, which were later linked to GPS location records. Eels, all observed very near the bottom, were counted only if they were within a transect that was defined by a viewing frame. Densities were calculated as eel counts/m<sup>2</sup> of transect, with confidence limits determined by a bootstrap procedure (ICES 2009).

American eel densities have been estimated from 39 GBB and 14 CMR surveys in bays, estuaries, lakes, barachois ponds, and freshwater impoundments in the southern Gulf of St. Lawrence (Tables 3 and 4). CMR density estimates and confidence limits were calculated by Bayesian analysis (Cairns et al. 2007). The mean percent difference of 95% confidence limits from the density estimate was, for lower limits, 53.3% for GBB and 30.9% for CMR, and for upper limits, 65.9% for GBB and 71.1% for CMR. Duration of field work for GBB surveys was one night per survey. Mean duration of field work for CMR surveys was 60.1 d per survey (SD 22.5, range 22-101). However, field parties conducted sampling for up to five CMR surveys concurrently, in comparison to one survey at a time for GBB surveys.

Eels observed in GBB surveys and captured in the fyke nets used for CMR sampling had similar length frequency distributions, with most eels  $\geq 30$  cm in length (Cairns et al. 2007, Hallett 2013).

The comparison in Tables 3 and 4 suggests that the GBB method is more time-efficient than CMR for estimating densities of American eels. GBB was marginally superior to CMR for upper confidence limits but markedly inferior to CMR for lower limits. GBB confidence limits would be improved by running surveys on consecutive nights and combining their results. Other considerations also impinge on decisions regarding survey methods. The GBB method requires visibility to the bottom. In Southern Gulf of St. Lawrence lentic habitats, the GBB window typically provided clear views of eels to 2.5 m and sometimes to 4 m depth in May and June.

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Within these depth ranges, objects on the bottom as small as a pencil lead can be readily seen. Later in the season, eutrophic plant growth often obscured visibility. Bog tannins may impair visibility. GBB observations do not record eels that are buried in the substrate or concealed in bottom debris. The typical perception of eels as nocturnally active/diurnally inactive is only an approximation of their diel cycle. The proportion of time during the night that American eels remain concealed in the substrate has not been accurately measured (Tomie et al. 2017).

Success of the CMR method depends on recaptures. In sites with low eel abundance, the number of recaptures may be insufficient to permit a population estimate with acceptable confidence limits. This means that a regional population summation based on a series of CMR surveys may be upwardly biased due to the non-inclusion of population estimates from sites with low eel abundance. The CMR method estimates population, not density, but conversion to density is possible if the effective area of the study site is known. In an enclosed water body with sampling sites distributed throughout, study site area is the area of the water body. If the study site has no distinct boundaries, such as a section of a large estuary, study site area can be estimated from eel home range, or from the distance that eels are likely to travel from capture sites. However, marking studies in the American eel report extreme variation in both home range (0.1 – 65 ha) and maximum linear displacement (0.05-16 km) (Cairns et al. 2012). For CMR study sites without distinct boundaries, uncertainty in study site area will decrease confidence in the conversion of population estimates to density estimates.

## **ABUNDANCE FROM BOAT ELECTROFISHING (CONTRIBUTOR: JOHN CASSELMAN)**

There is an increasing need to acquire eel abundance data, not only to assess presence and status, but to document abundance and habitat associations. More refined methods are needed for measuring density beyond simple entrapment methods that capture active fish. Capturing eels in a quantitative way is difficult, especially since they are elusive, most active at night, and in daytime hide under cover (e.g. rock rubble and woody debris) or by burrowing in soft substrate obscured by dense vegetation. Electrofishing is a well-established tool for capturing and assessing fish abundance and community associations (Reynolds 1983; Casselman and Grant 1998). Backpack electrofishing, used by wading field staff in shallow water, is widely used to quantify eel abundance in confined waters, using both point and transect sampling methods (Reid 2011). Boat-mounted boom electrofishers are well suited to open-water systems (Casselman et al. 1990), particularly since the method samples fish from their specific microhabitats.

Open-water electrofishing has been used as a commercial harvest tool in the east end of Lake Ontario commencing in the early 1980s (Casselman 2003). This method has been adapted to quantitatively sample eels along transects, providing comparable long-term data series in eastern Lake Ontario and the upper St. Lawrence River that assess numerical and biomass yellow eel densities (Table 5, Fig. 9). Open-water transect electrofishing methods have also been used to assess an experimental eel stocking program in the upper St. Lawrence River and eastern Lake Ontario (Pratt and Threader 2011). Electrofishing can damage eels (Reynolds and Holliman 2004); however, if conducted with proper operating conditions, using pulsed DC and low amperage, eels and other species can be electrofished safely (Casselman and Grant 1998, Casselman and Marcogliese 2014).

The quantitative methods used by Casselman and Marcogliese (2014) involve open-water electrofishing techniques to index eel density and abundance, as well as fish-community and microhabitat associations. These involve night- and daytime surveys incorporating replicate 100 m transect sampling by habitat type (upper St. Lawrence River 23 transects, eastern Lake Ontario 36 transects), which provide statistically valid measures of numbers and biomass on an

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area basis. The width of the effective electrified field is measured to ensure that the transect width is known and standardized and involves an effective field that neither attracts nor repels the fish but momentarily stuns them for recognition, sizing, and effective dipnet capture. In these surveys, missed or escaped eels are included as part of the catch if they fall within the transect. Calm-water nighttime electrofishing is most effective, particularly if high-intensity immersion lighting is used and if the effective field is marked with fluorescent trailers. Onboard computerization is used, integrated with timestamps and crew-specific audio files to document observations and activity. Activities are recorded in audio files that are analyzed to confirm computerized field records. Electrofishing transects are overlaid on Google Earth GPS real-time records. GPS waypoints are recorded for all electrofished eels, so fish community and microhabitat associations are precisely known. GoPro video files are collected, capturing the effective electrofishing field. All this requires reasonable water transparency and visibility. If visibility is limiting, such data are less informative. Ideal conditions, which have existed in the St. Lawrence River system since the zebra mussel invasion, involve transparency that allows the bottom to be visible in up to approximately 3.5 m of water, which corresponds to the maximum depth of effective electrofishing for this boat-operated open-water electrofishing method. Approximately three to four times as many eels are detected in nighttime compared with daytime electrofishing. Electrofishing from the night-to-morning crepuscular period is most effective because at that time eels are usually out of their cover and more easily seen, sized and, if sampled for biological data, dip-netted.

Since visibility is an important part of this survey method, it has parallels to visual surveys conducted with either scuba gear or a glass-bottom boat (see Abundance from Glass Bottom Boat section); however, it affords the additional advantage of making the eels more readily detected by virtue of response to the electrified field. Size of eels can be estimated visually, but electrofishing provides the opportunity to collect the eels to acquire precise biological data for safe subsequent release or lethal sampling. Electrofishing is best conducted in moderate-to-low conductivity water. Conductivity is usually site-specific, and test electrofishing can be used to standardize operating conditions and measure and adjust the effective width of the electrified field and the area covered by making adjustments to amperage and/or altering the surface area of the anode by adjusting immersion depth. These techniques have been used to “swim” eels in historic commercial fisheries and developed to semi-immobilize them in research surveys, the latter providing consistent and long-term indices indicating changes in abundance in the upper St. Lawrence River and Lake Ontario (Table 5, Fig. 10).

Electrofishing is a precise technique of sampling eels and has a much lower observational sampling variability than other techniques except for peak eel-ladder passage (comparable CVs: eel ladder 16–18%, electrofishing 20–24%, bottom trawling 95–118%, trap nets 110–250%, fyke and hoop nets 140–310%; from Casselman and Marcogliese, unpublished data). Thus, if appropriately replicated, electrofishing can detect changes in abundance more precisely than other open-water sampling techniques. As with most eel sampling techniques, electrofishing is ineffective in fast-flowing water since the stunned fish can be quickly swept away from the electrified field. Boat-mounted electrofishing is most effective if the rate of travel is such that the eels are exposed to the electrified field for approximately 3 to 6 seconds; recovery time is directly related and similar. Less exposure makes recognition and capture difficult; greater exposure lengthens time of recovery and, if extreme ( $\geq 10$  seconds), has the potential to injure the eel, causing vertebral column damage and associated haemorrhage (Casselman, unpublished data).

It would be useful to compare quantitative boat electrofishing with the glass bottom boat and net enclosure methods described elsewhere in this paper. Open-water electrofishing is a method of sampling that has potential for broader use in assessing eel status and abundance. Currently

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available electrofishing equipment is effective only in low-conductivity water. However, tests of a prototype boat-electrofishing system showed electrofishing effectiveness in brackish, although not full-strength salt, water (Lieschke et al. 2019). Further development and commercialization of this technology might open the option of using boat electrofishing to measure abundance of American eels in saline habitats.

## **ABUNDANCE FROM NET ENCLOSURES (CONTRIBUTORS: MALTE DOROW AND JENS FRANKOWSKI)**

The concept for this method derives from yellow *Anguilla* eels' in-substrate and near-substrate habitat use, their relatively small home range, and their largely nocturnal activity cycle (Baras et al. 1998, Tesch 2003, Barry et al. 2016, Tomie et al. 2017). It is also known that yellow eels stay burrowed after feeding events (Moriarty 2003).

Against this background, a transportable enclosure method (Fig. 11) was developed to estimate yellow eel density in the non-tidal coastal waters of the Baltic Sea (Ubl and Dorow 2015). An area of 1 ha is enclosed by a 1.8 m high boundary net with fyke nets in each corner. To increase the likelihood of capturing enclosed eels, six fyke net chains are deployed within the enclosed area. Mesh sizes are 10 mm for the boundary net and 11 mm for funnels of the corner and chained fyke nets. Nets with these mesh sizes are expected to be a complete barrier to passage of eels of length >36 cm (Bevacqua et al. 2009). The boundary nets and the corner fyke nets are transported separately to the fishing location. In a first step, one corner fyke with 12 m long lateral wings is fixed by an anchor. Then, a boundary net is attached with snap hooks to one of the lateral wings. As this attachment is done on the boat, the length of the lateral wing limits the fishing depth to 12 m.

Captures are expressed as yellow eels caught per ha over a soak time of 48 h, and are used for comparison between habitats or between time periods on a relative scale (Ubl and Dorow 2015). In general, three people are needed to set up and tear down the enclosure, with two working in a boat and one remaining on shore. Depending on the fishing location and distance to the shore, setting up/tearing down an enclosure system takes about two hours. Additional time is needed to document the harvest. Having two complete enclosure systems, the current standard fishing protocol allows the surveying of four sampling points (i.e. 4 ha) per week (Monday-Friday).

### **Enclosure evaluation**

Starting in 2008, tests in various habitat types demonstrated the applicability of the approach for yellow eel monitoring in the German sector of the southern Baltic Sea. Based on these trials, eight reference areas were defined, within which six randomly selected points are fished per year, for a total of 48 fishing points per year. Biological data are recorded for captured eels, allowing, for example, the calculation of Durif et al's. (2005) silvering index.

In 2015 and 2016, studies were undertaken to enable conversion of raw catch rates to eel densities. Telemetry data (Dorow et al. 2019) showed that eels in the enclosure moved back and forth along the boundary net, leading to potential capture in a corner fyke net, or away from the boundary net, leading to potential capture in the fyke net chain. The boundary net also poses an obstacle to the entry of eels into the enclosure. The proportion of enclosed eels captured after 48 hours was estimated by a three-pass removal experiment with 10 replications (Dorow et al. 2020). The enclosure was controlled for eels after 48, 72 and 96 hours. Hierarchical Bayesian modeling was used to analyse the removal data accounting for unequal individual eel catchabilities and the varying effort between the controls. On average 39% of enclosed eels >36 cm were captured after 48 hours soak time. Accordingly, yellow eel density

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can be estimated by applying a correction factor of 2.6 to eels per ha caught in standardized monitoring.

The enclosure method has been evaluated only in non-tidal coastal waters. Current flow in tidal waters might cause barrier nets to lean, affecting their capacity to retain eels. Possible modifications to the technique include higher boundary nets or longer soak times to capture a higher proportion of enclosed eels. Factors to convert raw enclosure captures to eel densities would need to be measured specific to environmental circumstances and gear details.

### **Monitoring results 2009-2018**

In total, 2,958 eels were caught at 427 monitoring points in eight reference areas in 2009-2018. Presence rate was 76.3% and yellow eels were detected in all reference areas. Silver eels were rare in catches (N=115, 3.8%; see Ubl and Dorow 2015). Of the 2,843 captured yellow eels most (81.3%) were harvested in the fyke net chains and most (80%) exceeded 36 cm in length.

Capture rates ranged from 0 to 107 eels (>36 cm) per ha. Capture rates of 20 per ha or higher were infrequent (N=24; 5.6%). Overall, mean capture rate for 2009-2018 was 5.3 ( $\pm$  9.1 SD) per ha, which gives a population density of 13.8 yellow eels per ha after application of the 2.6x correction factor. Given a mean weight of 267 g for yellow eels >36 cm (Ubl and Dorow 2015), the mean yellow eel biomass density along the German coastline of the southern Baltic is 3.7 kg/ha (>36 cm).

### **Conclusion**

The approach outlined above allows estimation of temporal and spatial variation in relative abundance and numerical and biomass densities, with accompanying biological data. Such information can be used for multiple purposes in eel population dynamics, including the estimation of eel recruitment to coastal waters and silver eel production. This approach has wide applicability to support eel stock assessments in the Baltic Sea and elsewhere.

### **DISTRIBUTION AND ABUNDANCE FROM ENVIRONMENTAL DNA (CONTRIBUTOR: CRAIG KNICKLE)**

Environmental DNA (eDNA) analysis, the detection of genetic material that organisms release to their environment, has emerged as a powerful tool in aquatic biodiversity assessment (Ruppert et al. 2019). The method involves field collection of water samples which are assayed by quantitative polymerase chain reaction (qPCR) to amplify and identify genetic material. eDNA has been shown to be particularly useful in the monitoring of invasive, elusive or endangered aquatic species (e.g. Boothroyd et al. 2016, Nevers et al. 2018). The use of eDNA to detect species presence is firmly established, but positive relationships between eDNA concentrations and organism abundance (e.g., Lacousiere-Rousel et al. 2015, Doi et al. 2017, Baldigo et al. 2017) suggest potential for eDNA to become a quantitative abundance indicator. However, eDNA concentrations depend not only on organism abundance, but on such factors as seasonal cycles of eDNA release, rates of eDNA degradation after release, and eDNA dispersion by water currents.

eDNA has aided understanding of Japanese eel (*Anguilla japonica*) distribution in fresh (Itakura et al. 2019) and oceanic (Takeuchi et al. 2019) waters, and shed light on ancient human use of New Zealand short-finned eels (*A. australis*) (Seersholm et al. 2018). Recent eDNA findings have failed to support hypotheses that the Loch Ness monster might be a catfish, a sturgeon, a shark, or a plesiosaur, and instead suggest that sightings interpreted as a monster might have been a [European eel](#).



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For the American eel, the scant knowledge of presence and relative abundance over most of the species' plausible range (Fig. 2) is a key obstacle to effective assessment and conservation. eDNA requires only water samples as field inputs, in contrast to conventional labour-intensive electrofishing, trapping, netting, and trawling. eDNA lab analysis has become routine and relatively low-cost, although protocols to reduce risk of cross-contamination may increase processing cost. The simplicity of eDNA in the field and lab makes it the only available method that is potentially capable of measuring the distribution and relative abundance of American eels to the species' western and southern limits, given current and foreseeable constraints of resource availability.

eDNA projects can be species-specific, but increasingly multi-species assays are used. The [Aquatic eDNA Atlas](#) compiles eDNA data for aquatic organisms in conterminous US states (Table 1). With the rapid expansion of the eDNA technique, coverage of crowd-sourced eDNA databases can be expected to soon extend over much or most of the plausible American eel range.

In conjunction with Parks Canada and the Helbing Lab of the University of Victoria, the Mi'kmaq Confederacy of Prince Edward Island is piloting a project to assess the feasibility of eDNA sampling as a tool to estimate relative American eel abundance in freshwater ponds in Prince Edward Island National Park. The study will examine the relationship between counts and biomass estimates from annual monitoring using traditional methods (trap nets) and eel eDNA concentrations over various spatial and temporal scales. A primer to identify American eel eDNA has been developed. It is anticipated that results will allow researchers to determine the effectiveness of eDNA sampling as a tool in estimating eel abundance and distribution that could be applied in other areas. A program to measure American eel eDNA in Quebec waters is also under development by the Quebec Ministère des Forêts, de la Faune et des Parcs (Dalie Côté-Vaillancourt, MFFP, pers. comm.).

## **ABUNDANCE FROM LARVAL SURVEYS (CONTRIBUTOR: MARTIN CASTONGUAY)**

A large number of abundance series are available for glass, yellow, and silver American eels (ASMFC 2017, Cairns 2020), but trajectories of these series are heterogeneous, making it difficult to derive an overall abundance trend for the species. The availability of quantitative larval survey data from the Sargasso Sea offers the possibility of tracking abundance change at the earliest stage of a cohort, before abundance is altered by geographically differing mortality or by shifts in the relative importance of migratory routes.

Hanel et al. (2014) reported that abundances of American and European eel leptocephali (indicated by catch rates, i.e. numbers per  $10^5\text{m}^3$  of water filtered by Isaacs-Kidd Midwater Trawl, IKMT) in the Sargasso Sea spawning site have declined by about an order of magnitude between the 1980s (two surveys) to 2011. Catch rates (mean $\pm$ SD) of American eels were  $19.6\pm 10.7$ ,  $7.9\pm 14.4$ , and  $2.0\pm 3.0$  in 1983, 1985, and 2011, respectively. Catch rates of European eels were  $27.5\pm 15.3$ ,  $7.8\pm 10.3$ , and  $1.4\pm 2.4$  in these three years, respectively (Hanel et al. 2014). Catch rates were significantly lower in 2011 than in 1983/1985 (t-tests,  $p < 0.001$ ).

However, this temporal comparison could potentially be biased by differences in sampling gears (8.7 m<sup>2</sup> IKMT mouth opening in 1983/1985 versus 6.2 m<sup>2</sup> IKMT in 2011), and in oceanographic features, which may tend to concentrate larvae in frontal regions where most sampling takes place (fronts were less well defined in 2011 than in the earlier period). As a check on these potential biases, Hanel et al. (2014) compared the abundance of other anguilliform leptocephali that were collected at the same sampling stations to determine if the relative abundance of

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*Anguilla leptocephali* had changed between the two time periods in comparison to the other species of leptocephali.

Hanel et al. (2014) found that even though that the leptocephalus assemblage was the same in the two periods, in 2011, *Anguilla* spp. (*rostrata* N=44, *anguilla* N=42, *rostrata-anguilla* hybrid N=1) were no longer the most abundant leptocephalus taxon but instead ranked fifth. Catches of the more abundant taxa of anguilliform leptocephali (*Nemichthys scolopaceus* (N=541), *Ariosoma balearicum* (N=531), *Serrivomer lanceolatooides* (N=144), and *S. beanii* (N=129)) were not consistently lower in 2011 compared to 1983/1985 and were not nearly as low as in the two *Anguilla* species (Hanel et al. 2014). The only exception to this was *N. scolopaceus* which declined as steeply as the two *Anguilla* species. Overall the data suggest that the abundance of American and European eel larvae in the spawning site declined by about an order of magnitude between the 1980s and the 2010s. This decline infers a similar decline in spawning biomass of the two *Anguilla* species.

Using more extensive datasets (with some overlap with Hanel et al. 2014), Westerberg et al. (2018) calculated that abundances of European eel leptocephali in the Sargasso Sea spawning site declined by 70-80% after 2007 compared to the 1980s and earlier. This decline is of the same magnitude as the decline in European eel commercial landings. Westerberg et al. (2018) further calculated that glass eel recruitment to Europe has decreased by ca. 95%, and even more for North Sea recruitment indices. They postulated that the greater glass recruitment decline compared to the leptocephalus decline reflects increased mortality at sea or a shift of glass eel arrivals to non-monitored regions, such as the Mediterranean Sea. It is noteworthy that the steeper recruitment decline in a northern part of the European eel distribution area (North Sea) parallels the more pronounced recruitment decline for the American eel in the St. Lawrence River basin. It is unlikely that the comparative method used by Westerberg et al. (2018) could be used with the American eel due to the paucity of glass eel recruitment series for this species.

The continuation of the American eel larval abundance series depends on future research cruises to the Sargasso Sea. The Thunen Institute of Fisheries Ecology (Hamburg, Germany) has an ongoing eel [research program in the Sargasso Sea](#), with a cruise planned for spring 2020, followed by further cruises at three year intervals (R. Hanel, Thunen Institute, pers. comm.). This series started in 2011, with following cruises taking place in 2014 and 2017. There was an additional cruise in 2015 from a different program using a different vessel. Hence the March/April 2020 mission to the Sargasso Sea will be the fifth such survey since 2011.

## **ANALYTIC RESOURCES AND TOOLS**

### **ENVIRONMENTAL DATABASES (CONTRIBUTOR: DAVID CAIRNS)**

Table 6 lists selected databases that provide environmental data that are relevant to eel habitat use and distribution. Habitat classifications by multiple environmental parameters are supplied by McManamay et al. (2018), Millar et al. (2019), and Noseworthy et al. (2019). Data on hydrography and watersheds are supplied by the Canadian National Hydro Network and the US National Boundary Dataset. Data on barriers are supplied by national Canadian and US dam inventories and by global inventories assembled by Global Dam Watch, Open Street Maps, and the International Commission on Large Dams.

The increasing reach and depth of such databases enable the development of models that explain and predict fish presence and abundance (Lassalle et al. 2009, Woods and McGarvey 2018). These approaches may potentially shed light on eel biology, distribution, and abundance over large geographic areas in which eel-specific field studies are sparse or absent.

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However, much of the data that could fuel advances in eel assessment science are not yet in publically accessible databases. Freshwater records of American eels are not yet comprehensively assembled in databases (see Mining of Range Records section). River connectivity is essential for eel access to fresh water, but most barrier databases cover only large and medium dams (Tables 6 and 7). Databases exclude millions of small dams worldwide (Liermann et al. 2012). Renwick et al. (2005) estimated 2.6 million small ponds in the conterminous US from satellite maps of 30 m pixel size, and 9 million small ponds from extrapolations of maps which show features with dimensions as small as 5 m. The great majority of these ponds are artificial (Renwick et al. 2005). Using a different methodology, Renwick (2017) estimated that there are about 0.5 dams of all sizes /km<sup>2</sup> in the conterminous US, for a total of about 4 to 4.5 million dams. The Open Street Maps database includes dams of all sizes, but coverage is incomplete. The number of dams from Open Street Maps and from national inventories for Prince Edward Island, Maine, and Puerto Rico are 61 and 0, 616 and 584, and 7 and 32, respectively. The Freshwater Network Barrier Database, which excludes dams on streams too small to be depicted on 1:100,000 topographic maps, lists 614 dams in Maine. In contrast, local studies show much higher numbers of dams for Maine (1,356 including historic dams, Hall et al. 2011) and for Puerto Rico (203, Cooney and Kwak 2013). These findings suggest that most dams, especially small dams, within the American eel range are not listed in any database. Barrier databases generally contain little, or more often no, information on passability of eels or other fish. A further limitation of database use in American eel assessment science is their sparse, and often null, coverage of American eel range outside of Canada and the US. Given the large number and wide distribution of unmapped dams, crowdsourcing may be the only viable path to documenting their locations and essential features ([amber.international/european-barrier-atlas/](http://amber.international/european-barrier-atlas/)).

In open marine waters, the availability of large environmental databases has spurred development of habitat classification schemes that cover broad geographic areas (O'Boyle 2009, Harris and Baker 2020). Much of the input data for these projects comes from survey series that use ocean-going research vessels to collect scientific data over large stretches of ocean under standardized protocols. In contrast, biological surveys conducted in the estuaries and sheltered bays that eels use as growth habitat tend to be conducted by local rather than national agencies (Cairns et al. 2017). This may explain the relative lack of development of databases and habitat classifications in estuary/bay waters compared to offshore waters (Allee et al. 2010, Greenlaw et al. 2011). Dutil et al. (2012) used a detailed database (103 descriptors) to classify coastal and epipelagic Gulf of St. Lawrence waters. However the cell size (6.25 km<sup>2</sup>) is too coarse for meaningful modeling of saline growth-phase habitat of American eels.

### **FETCH AS A COVARIATE OF ABUNDANCE (CONTRIBUTORS: DAVID CAIRNS AND DERYCK MILLS)**

A substantial but unquantified portion of American and European eels use saline (salt and brackish) water as growth habitat (ICES 2009). Saline waters produce most of the American eels currently harvested in Canada and nearly all the eels commercially harvested in the US (Fig. 1; Cairns 2020). American eels commonly use bay and estuarine habitats but there is little precise knowledge of occupancy patterns and seaward distributional boundaries (Pratt et al. 2014). Cairns et al. (2017) compiled American eel records from 26 bottom trawl and beach seine surveys in North American waters between Labrador and Florida (see Mining of Range Records section). In some areas, coverage of compiled surveys is sufficient to indicate broad patterns of relative eel abundance in saline waters, but in other areas information is too scant to confirm patterns. Other data sources suggested in this paper may improve our knowledge of eel distribution in saline waters, but large areas will inevitably remain without direct knowledge. What is needed is an approach in which eel relative abundance (or density) in well studied

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areas can be related to physical or other factors that have been measured across broad areas. With such relations in hand, eel relative abundance can be predicted or modeled in areas where direct measurements are unavailable.

Fetch is the straight-line distance between a point, at sea or along the coast, to land in a given compass direction. Mean fetch is the mean of such measurements taken in multiple compass directions. Mean fetch serves as a proxy for the degree of exposure to the open sea. Winds usually blow more often from certain directions. To better reflect exposure conditions, mean fetch calculations are often adjusted by the frequency distribution of wind directions. Mean fetch commonly explains a substantial fraction of the variation in coastal biological communities (Callaghan et al. 2015, Longtin et al. 2016, Smale et al. 2016).

High-resolution mapping of mean wind-adjusted fetch in eastern North American waters has recently been completed (D.K. Cairns and D.E. Mills unpubl.) (Fig. 12). Mean fetches were calculated for the centroids of 50 m x 50 m cells up to 5 km from the coast, and for 200 m x 200 m cells between 5 km from the coast and the 500 m bathymetric contour. In the course of this work it was discovered that the accuracy of fetch mapping falls off sharply with low sample sizes in inshore and semi-enclosed waters. Previous ecological studies calculated mean fetch from fetches measured in 16 to 48 compass directions. Maps of mean fetch calculated with this range of sample size contain anomalous ridging patterns which are artefacts of the method. To avoid these artefacts, the new fetch map calculated means from individual fetches measured in 360 compass directions.

Cairns et al. (2017) found a generally declining relation between standardized eel catches per trawl haul and mean fetch, with mean fetch calculated in 36 compass directions. This is consistent with long-standing qualitative observations that growth-phase eels are more abundant in sheltered water. The relation between eel abundance and mean fetch may be further examined by re-analysis of the Cairns et al. (2017) dataset using mean fetches calculated from a greater number of compass directions, and from other data sources indicated in this paper. If a consistent relation between relative abundance and mean fetch can be established, the availability of the new fetch map will permit relative eel abundance to be modelled along the entire east coast of North America. However, fetch is only one environmental parameter that might assist in predicting American eel distribution. More accurate predictive models will require development of databases that encompass a suite of environmental variables for bay and estuarine habitats occupied by eels (see Environmental Databases section).

Mean fetch is a reasonable approximation of exposure to the open sea, but sea exposure can be more exactly calculated by physical models that also embrace wave dynamics and bathymetry (Callaghan et al. 2015). The advantage of fetch is that it can be calculated solely from a coastline map, without need for site-specific oceanographic studies. The accuracy of inshore fetch mapping depends on the accuracy of the coastline map. The new fetch map is based on coastline maps with scales of 1:50,000 (Canada) and 1: 5,000-20,000 (eastern US) (Cairns et al. 2017). Base maps for the US Gulf of Mexico coast are expected to be available at similar scales as the eastern US. Availability of high-resolution maps for Mexican and Caribbean coastlines has not been explored.

Community composition of fish and other biota has also been shown to be related to mean fetch in fresh water (Chu et al. 2014, Nohner and Diana 2015, Cazenave et al. 2016), which suggests the potential to use fetch to help understand and model American eel distribution in lakes and large rivers.

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## **ACCOUNTING FOR NET EFFECTS OF SMALL DAMS (CONTRIBUTOR: DAVID CAIRNS)**

### **Dam impacts and numbers**

Dams are a major theme in the conservation science of freshwater fish, including eels. Most attention has been focused on connectivity, a critical element of freshwater ecology that enables organisms to navigate river axes to meet their life history needs (Leibowitz et al. 2018). Dams may impair eel passage in both upstream and downstream directions (Haro et al. 2000, Cooney and Kwak 2013, Woods and McGarvey 2018). Yellow eels that successfully ascend hydro dams face risk of turbine mortality on their descent toward the sea as silver eels (Carr and Whoriskey 2008, Sweka et al. 2014). Dams may further harm fish communities through alteration of watercourse flow, temperature, nutrient, and productivity regimes (Macnaughton et al. 2017).

Most studies of dam effects on eels have taken place at medium and large dams, whose distribution and numbers are well known (Table 7, Shin et al. 2019). National inventories list 1,157 large dams in Canada and 91,470 in the US (Table 6). Small dams are much more numerous than medium and large dams (Liermann et al. 2012). Lentic water bodies (lakes and ponds, both artificial and natural) in the US have been estimated to number >2 million, 2.6 million, 4.5 million, 6.6 million, and 9 million, using various methods and various criteria for inclusion (Table 7). The great majority of these water bodies are small ponds. The proportion of small ponds in the US that are formed by dams has not been accurately measured. Smith et al. (2002) considered that most of these ponds were formed by dams, and Renwick et al. (2005) stated that small ponds are "overwhelmingly of human origin." Renwick et al. (2005) further estimated that 21% of the drainage area of the conterminous US flows through small ponds. These findings support the view that small ponds formed by dams may be ecologically important, and that only a small fraction of them are recorded in inventories. Comparisons of national databases (Table 6) and local enumerations for Wisconsin and Utah (Poff and Hart 2002), Maine (Hall et al. 2011), and Puerto Rico (Cooney and Kwak 2013) likewise suggest that inventories account for only a small fraction of dams.

Noting that impacts of small dams do not necessarily mirror those of large dams, Gangloff (2013) reviewed literature on the ecological effects of small dams and found both positive and negative effects (see also Ebel and Lowe 2013 and Holcomb et al. 2016). On this basis, Gangloff (2013) argued that a holistic approach to understanding small dam effects involves assessing both positive and negative impacts. In contrast, Birnie-Gauvin et al. (2018) maintained that a holistic approach to dams requires their removal wherever possible.

### **Dam impacts on Prince Edward Island**

This study uses data from Prince Edward Island (PEI), a 5,660 km<sup>2</sup> island on Canada's east coast, to shed light on whether small dams might be important to eel conservation in positive (benefits) and/or negative (harms) directions. In particular, it considers a factor not previously raised in eel literature, which is that most dams widen streams and rivers into broad impoundments and reservoirs, thereby increasing aquatic habitat.

Eels are habitat generalists that can use both flowing and non-flowing waters (Pratt et al. 2014, Lloyst et al. 2015). For eels to benefit from the increase in aquatic habitat caused by dams, it is necessary that they be capable of upstream movement into such habitat, and of downstream exit on their seaward migration as silver eels. In addition, the habitat created by dams must be suitable for eels.

This study uses two approaches to evaluate eel movements and populations in relation to PEI dams. Study areas are bays and estuaries and inflowing streams that have dams in their lower

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reaches. First, movements between four impoundments and their receiving bays/estuaries were inferred from otolith strontium-calcium ratios, which reflect changes in ambient habitat salinity during a fish's lifetime. Previous studies have shown that American eels in northeastern North America commonly exhibit bi-directional movements between fresh and saline waters (Jessop et al. 2008). McCallums Pond drains into Brackley Bay over an earthen dam with a 2.2 m vertical-drop spillway (Lamson et al. 2006). There is no fishway. Cass Pond, head 0.9 m, drains into Covehead Bay via a spillway and a pool-and weir concrete fishway. Marshalls Pond, head 5.0 m, drains into Covehead Bay via a 303 m rocky-bottomed channel with 1.7% slope. Whitlocks Pond drains through a spillway and a rocky channel to a 2.5 km stream reach to a further pond (Ross Pond), which drains through a rocky channel to the Boughton River Estuary (Cairns et al. 2004).

Sr:Ca ratios indicate that eels commonly transited in both directions between Cass and Marshalls Ponds and the receiving bay (Lamson et al. 2006). In McCallums and Whitlock Ponds, Sr:Ca ratios indicated that sampled eels entered fresh water in their elver year and did not subsequent transit between fresh and saline waters (Cairns et al. 2004, Lamson et al. 2006).

Movements and populations in relation to dams were also evaluated using density estimates in PEI impoundments, bays, and estuaries, derived from glass bottom boat surveys and capture-mark-recapture experiments (see Glass Bottom Boat section). Mean densities were 188.1 eels/ha (SD=198.0, N=18) for bays and estuaries and 142.5 eels/ha (SD=159.7, N=4) for impoundments (ANOVA  $F=0.18$ ,  $P=0.68$ ) (Tables 3 and 4). Four locations had density estimates for impoundments and bays/estuaries on the same system. The mean density (eels/ha) in bays/estuaries (130.2, SD=96.0, N=4) did not differ significantly from that of impoundments (143.3, SD=159.6, N=4) (paired t-test,  $P=0.820$ ) (Fig. 13).

Dams are numerous on PEI and have substantially increased freshwater interior habitat. Cross-salinity movements inferred by otolith microchemistry and comparisons of density estimates suggest that at two locations eels readily access impoundments and occupy them at roughly similar densities to bays and estuaries. At these locations, dams may provide a net benefit to eels. At two other locations, otolith microchemistry data suggest that dams form an age-specific barrier, limiting upstream access to eels in their first continental year. Such a finding may be due to the ability of eels <10 cm in length, but not longer, to creep up rough vertical surfaces (Legault 1988). Further caveats to these findings apply. Density measurements of impoundments are few (N=4), and neither densities nor otolith microchemistry data are available for headwater reaches of PEI streams.

### **Implications for dam-related conservation science**

Estimated dam density for the conterminous US is 0.5 dams/km<sup>2</sup> of land (Renwick 2017). The US National Wetlands Inventory (NWI) maps 21,777 km<sup>2</sup> of fresh aquatic habitat without emergent vegetation in US Atlantic drainages, including the St. Lawrence system (Cowardin et al. 1979 and Dahl et al. 2009; data compiled by Cairns et al. 2014). Of this total, 1,129 km<sup>2</sup> (5.2%) is classed as tidal riverine, 2,728 km<sup>2</sup> (12.5%) is classed as riverine, 14,590 km<sup>2</sup> (67.0%) is classed as lacustrine (lakes), and 3,330 km<sup>2</sup> (15.3%) is classed as palustrine (ponds). Together, these data suggest that there is more lentic (lake and pond) than lotic (riverine) habitat in the American eel range in US Atlantic states, and that there is more pond habitat than non-tidal riverine habitat.

There is a well-developed science that documents negative effects of dams on fish (e.g. Leibowitz et al. 2018) and there are active campaigns to remove dams (e.g. damremoval.eu). At the same time, there is a science that deals with the creation and management of small

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impoundments for conservation purposes, including enhancement of fish populations (Eades and Lang 2012, Neal and Willis 2012, Schramm and Willis 2012). There appears to be little interchange between the literature on negative effects of dams on fish and the literature on building and managing impoundments to benefit fish.

The large quantity of lentic habitat in the American eel range in the eastern US (and perhaps elsewhere) implies that such habitat may play a substantial role in overall freshwater production. The effect of dam-induced increases in aquatic habitat has not previously been considered in eel literature. Data reviewed in this section suggest that effects of small PEI dams may be both positive (by creating additional habitat that eels can and do use) and negative (by limiting upstream passage) effects. The availability of evidence for both benefits and harms of small dams to eels supports Gangoff's (2013) contention that a holistic evaluation of the impacts of small dams should be open to both positive and negative effects. A holistic approach would draw on findings and insights from literature on impoundments constructed for conservation purposes (Neal and Willis 2012) as well as literature on negative effects of dams on fish (Leibowitz et al. 2018).

Spatially explicit eel stock assessments require an understanding of the dynamics of upstream movements and habitat use. Upstream movement can be modelled as a diffusive process (Smogor et al. 1995, Ibbotson et al. 2002, Lambert et al. 2011). This produces densities that decline with distance from sea, although it is not certain whether density itself is the driver of upstream movements (Ibbotson et al. 2002). Lower eel densities above dams are generally interpreted as a consequence of restricted upstream passage at the dam (Cooney and Kwak 2013). Factors reviewed in this section suggest a broader range of possibilities for consideration:

1. Dams may impair upstream passage completely, partly, or not at all, and passage impairment may be size-dependent.
2. The power function that predicts watercourse width from upstream watershed area has been used to estimate eel habitat (Thornton et al. 2007, Lambert et al. 2011). Because dams typically widen watercourses and increase wetted area, this function will not provide reliable estimates of wetted habitat upstream of dams.
3. Eels entering an impoundment will typically encounter a greater amount of habitat than the original watercourse. This larger amount of habitat will lower their density. If pressure to move upstream is mediated by density, then the number of eels moving upstream from an impoundment will be lower than the number moving upstream from the original stream reach prior to dam construction. Consequently, a decline in stream densities in upstream reaches, in comparison with densities in the original unimpounded system, does not necessarily indicate that the dam is reducing the ability of eels to access upstream waters.

Lambert et al. (2011) developed a model called Obstacle Mitigation Model for Eel in Rivers (OMMER), which they tested in the Rimouski River, Quebec. OMMER divided the watercourse network into 1,376 compartments and modeled movements according to a diffusion function. Passage impairment at barriers was estimated primarily from barrier height. The authors noted that the presence of lakes in the system (whose area was 6-fold larger than riverine area) decreased eel density. However, areas of lakes and impoundments were not treated in the model. Models developed for European eels in France (Anon. 2018, Briand 2018) and for New Zealand longfin eels (Beentjes et al. 2016, Hoyle 2016) likewise do not incorporate areas of lakes and impoundments.

Assessment of eels in fresh water typically relies largely on counts of eels through migratory passways and on backpack electrofishing, which is limited to wadeable waters. Assessment

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efforts that take full account of effects of dams will require better understanding of eel use of lentic waters. Field and analytic tools treated in this paper may aid such an endeavor.

### **DEVELOPMENT OF A PILOT GIS-BASED HABITAT MODEL (CONTRIBUTORS: JOHN YOUNG, ALEX HARO AND HEATHER GALBRAITH)**

The Atlantic States Marine Fisheries Commission (ASMFC) conducts stock assessments for American eel in support of its fisheries management responsibilities for Atlantic coastal states. The most recent assessment was conducted in 2012, with an update in 2017 (ASMFC 2012, 2017). However, a review panel did not accept the modeling approach used (Depletion-Based Stock Reduction Analysis) for management use. Subsequently, ASMFC asked the US Geological Survey - Leetown Science Center (USGS-LSC) to examine whether and how geographic information system (GIS) based habitat assessments could aid stock assessment activities, and particularly if habitat information could inform estimates of eel population size, sex ratios, and/or biomass. A scoping exercise included reviews of previous habitat requirement studies, modeling of eel congeners in other parts of the world, and examples from other studies that based biomass and carrying capacity estimates on GIS-based habitat assessments. USGS-LSC proposed a phased approach that would entail inventory and data compilation, focused pilot studies in data-sufficient areas, and (ultimately) a range wide-assessment.

At this pilot stage, the project aims to build a modeling framework that will identify and track key features of the status and dynamics of continental phase American eels in the general region of Delaware and Chesapeake Bays. Datasets for freshwater model input include the National Hydrography Dataset, StreamCat, the Northeast Aquatic Connectivity Assessment Project, the National Wetlands Inventory, and state electrofishing data collections. For saline waters, inputs will include bathymetry from a new seamless topobathymetric elevation model, research trawl datasets, and a high resolution fetch database (see Fetch as a Covariate of Abundance section). Models, written in R, will build on previous European and New Zealand modeling experience. Potential analytic tools include generalized linear modeling, generalized additive modeling, boosted regression trees, and random forest methods. GIS will provide a platform for spatially explicit analysis that recognizes, for example, sex ratio variability with position in the drainage area. The long-term goal is to build a modeling framework that can be broadly expanded in the American eel continental range.

### **SPATIO-TEMPORAL NEW ZEALAND MODEL (CONTRIBUTORS: SIMON HOYLE, MERRILL RUDD, SHANNAN CROW, JAMES THORSON, AND ERICA WILLIAMS)**

#### **Background**

The endemic New Zealand longfin eel (*Anguilla dieffenbachii*) supports important commercial, customary (indigenous) and recreational fisheries in New Zealand, and is a key species in freshwater ecosystems. Longfin eel stocks have been affected by fishery removals, the eel destruction campaigns of historic acclimatisation societies that aimed to establish trout and salmon populations, habitat destruction and modification, barriers to upstream fish passage, and direct mortality from hydroelectric turbines, flood control schemes and drain clearance activities.

A 2013 international review of information relating to longfin trends and status emphasised the need for knowledge on stock size and the processes structuring longfin populations (Haro et al. 2015). The review panel recommended the development of a comprehensive longfin eel population assessment in New Zealand, which could then be used to help sustainably manage this stock.



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Longfin population assessment models cannot easily be developed using conventional methods because eels have a complex life history pattern and stock structure (Dunn et al. 2009). Eel stocks are distributed fractally during their freshwater phase, with diverse growth rates, sex ratios, and length and age compositions at many spatial scales, and low movement rates between areas. Management typically occurs via spatial fishing access and catch rules, which requires knowledge of the distribution of potential spawners and their access to the sea, so that sufficient spawning escapement can be maintained. A review of stock assessment methods for longfin eels (Hoyle 2016) recommended the development of a spatially distributed modeling approach to integrate information from multiple sources and predict the female spawning biomass of longfin eels. This requires both fishery and fishery independent data. Fished areas are likely to have different population structures from unfished areas, with the majority of female spawning biomass supported by unfished areas (Hoyle and Jellyman 2002).

The aim of the present project is to develop a modeling framework that can be used to estimate longfin population structure across New Zealand.

## Methods

The modeling framework comprises estimation and prediction components, with much of the progress thus far on the estimation component.

Preparing the estimation models requires four major steps: 1) develop the spatial framework; 2) prepare all relevant population data; 3) develop and fit the estimation model; and (4) determine the management targets and control rules associated with results from step 3.

The New Zealand River Environment Classification (REC) network database (version 2.4) is used as the spatial framework. The REC is based on a digital drainage network that was derived from a digital elevation model (Snelder and Biggs 2002). The digital network represents New Zealand's rivers as ca. 600,000 segments (bounded by upstream and downstream confluences) and their corresponding catchments.

The REC network is populated with relevant available information, including information on encounter/non-encounter from the New Zealand Freshwater Fish Database (NZFFD), abundance, environmental conditions, and habitat characterisation.

The estimation models use a spatio-temporal modeling approach based on the Vector Autoregressive Spatio-Temporal (VAST) program (Thorson and Barnett 2017). VAST is an R package for implementing a spatial delta-generalized linear mixed model (delta-GLMM) with many features such as density covariates, catchability covariates, and multiple categories (e.g. species, size, or age classes). It is designed to estimate spatial variation in responses using spatially-referenced encounter, count, or biomass data, with the goal of estimating the density across space and in one or more years by modeling probabilities of occurrence and positive catch rates as the two components of an [underlying delta model](#)

Characteristics of stream networks are highly correlated in space and time. However, two points along the network are not necessarily related based on their Euclidean distance, but on their network connectivity. Therefore, the standard VAST approach of using a triangulated mesh to relate observations based on Euclidean distance would not appropriately model populations along a stream network. Stream data has natural knots where segments join that can be used to define the network knots in relation to observations. To take advantage of the many features already implemented in VAST (e.g. covariates, multivariate models), we added an additional spatial model to VAST that relies on the Ornstein-Uhlenbeck (OU) process to describe autocorrelation based on distances along stream networks. Hocking et al. (2018) recently implemented the OU algorithm in a custom-built, hierarchical, spatio-temporal model of brook

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trout densities in Pennsylvania. In developing the framework, we have applied it to longfin eel encounter rate data from two catchments as case studies: the Waitaki and the Waikato, as well as an additional case study of Oregon coastal coho salmon using a multivariate model relating spawner and juvenile densities. These studies are currently being written up.

## **Prospects**

The long-term goal is to estimate a proxy for female spawning biomass by using the spatiotemporal models to predict both density and the proportion of the population that is female and likely to mature within a defined period. The VAST models using encounter/non-encounter data estimate a probability of occurrence which can be used as a proxy for spatio-temporal density. Sex ratios of longfin eels are available for some areas in New Zealand. Where they are not available, we will use assumed values based on expert opinion, or on the assumptions implicit in current modeling approaches. VAST has also been used to fit to presence/absence, count, and biomass-sampling data (Grüss and Thorson 2019), so we will also inventory available data using either eel counts or biomass samples to combine with available encounter/non-encounter data.

Intermediate project goals are to identify eel sampling data requirements for different approaches to estimation and levels of uncertainty. Where estimates are not available or achievable, we will use assumed values based on expert opinion, or on the assumptions implicit in current modeling approaches.

## **GLASS EEL RECRUITMENT AS AN ASSESSMENT FOUNDATION (CONTRIBUTORS: VIRGINIE BORNAREL AND HILAIRE DROUINEAU)**

Fisheries and Oceans Canada assesses the status of American eel and sets abundance targets based on trend analysis of abundance indices (DFO 2014). Composite indices were developed for a combination of life stage, habitat and Recovery Potential Assessment zones, but not for eastern Canada as a whole, as the zonal weights needed to calculate such an index are unknown. In the US, the Atlantic States Marine Fisheries Commission (ASMFC) generates Atlantic coast-wide abundance indices for young of the year (YOY) and yellow American eels by combining individual standardized indices into a coast-wide index. However, trends in abundance indices vary within and among sites (ASMFC 2017), and differences in gear type and placement and survey site locations may result in different catchabilities with consequent effects on data comparability among sites (ASMFC 2012). For these reasons, coast-wide indices may not reliably reflect abundance changes for that portion of the population.

In Europe, recruitment trends are among the indicators used by the Working Group on Eels (WGEEL) to assess European eel stock status. However, WGEEL faces the same challenges in the development of a range-wide abundance index as those found for the American eel. In response, Drouineau et al. (2016) and Bornarel et al. (2018) developed and implemented a model, termed Glass Eel Recruitment Estimation Model (GEREM) (Fig. 14). GEREM uses Bayesian techniques to estimate absolute annual recruitment at three nested spatial scales: at the river catchment level, at an intermediate spatial scale (i.e. a zone) and at a larger scale over the whole study area. This allows recruitment at larger scales to be inferred from observations carried out at the catchment level. A zone is composed of a specific number of catchments. GEREM uses estimates of absolute recruitment available at the catchment scale to extrapolate abundances to all other catchments of the zone. A weighting factor is calculated for each catchment as a power function of its surface area assuming that catchment attractivity is related to discharge (Burgers et al. 2014). GEREM can use time series of relative recruitment, from fisheries-dependent and -independent sources, and also estimates of absolute recruitment or observations from which absolute recruitment can be inferred. Time series of relative

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abundance are used to inform the temporal trend in the zone. Zonal recruitments are then summed to derive the overall recruitment over the study area. Three criteria must be met: 1) catchment recruitment within a zone must follow a similar trend, 2) catchment recruitment within a zone must follow a similar “catchment weight vs. catchment surface area” rule (i.e. similar densities of glass eels within a zone), and 3) at least one time-series or point estimate of absolute recruitment is required per zone.

GEREM has been applied to a large portion of the European eel range to yield a single recruitment index for this area (Bornarel et al. 2018). GEREM has also been implemented in southwestern Japan (Yokouchi et al. unpublished) and is currently used in projects in Spain, France and Portugal and Britain. An upcoming project aims to couple GEREM with Eel Density Analysis (EDA), which is oriented to yellow eel abundance, to better relate recruitment and standing stock and enable predictions of yellow eel abundance and silver eel escapement in southwestern Europe.

Since 2000, ASMFC has required Atlantic states to conduct annual YOY surveys (ASMFC 2000). Additional indices that are not mandated by ASMFC are also used in the US stock assessment (ASMFC 2017). Most surveys are standardized by GLM to account for changes in eel catchability. This produces valid indices of relative abundance that could be used for a potential application of GEREM to the American eel. However, no absolute abundance series or estimates are available. In Canada, glass eel recruitment has been measured at East River Chester, near Halifax, Nova Scotia, in 1996-2002 and 2008-present. Counts are deemed to be complete counts of glass eels entering the river. These counts, coupled with data from commercial fishing effort and harvest in the nearby estuary, yield estimates of the total run of glass eels toward the river (DFO 2014). East River Chester provides the only ongoing glass eel abundance series in Canada. In the Gulf of St. Lawrence, exploratory attempts to set up glass eel monitoring programs have typically produced very low counts, often with catch rates at or close to zero (Dutil et al. 2009, D. Cairns unpubl. data). Glass eel recruitment estimates and series are unavailable for the Gulf of Mexico and the Caribbean Basin. Some Caribbean commercial landings data are available (Cairns 2020), but these series are short, of uncertain reliability, and do not have a known relation to glass eel abundance.

Application of glass eel recruitment-based assessment modeling to the Atlantic coast of North America will require development of absolute glass eel series in the US, and abundance series with wider geographic coverage in Canada. The approach used by Bru et al. (2009) may be helpful in generating absolute abundance estimates from relative abundance measurements.

Extension of a glass eel recruitment-based approach to the full species range will require abundance series in the Gulf of Mexico and the Caribbean Basin, where the American eel is broadly distributed (Benchetrit and McCleave 2016). Developing such series will require substantial effort, and will need at a minimum to cover locations where American eels appear to be most abundant.

Since continental-stage American eels are fragmented in small units with contrasting environmental conditions, life history traits and anthropogenic pressures, it remains difficult to assess yellow and silver eel stages at a larger scale. Glass eel recruitment to catchments can be monitored at a single point at a river mouth, and GEREM provides a coherent tool for analysis over broad geographic scales. For these reasons, monitoring at the glass eel stage may be a feasible option to build the abundance series that will be needed for an eventual range-wide American eel assessment.

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## ESTIMATING AGE STRUCTURE FROM LENGTH STRUCTURE (CONTRIBUTOR: XINHUA ZHU)

Age composition is a critical source of information for understanding biological processes of growth, mortality, recruitment and migration, as well as sex-specific estimates of fish population parameters (Weatherley and Gill 1987, Quinn and Deriso 1999). Many fish species can be aged by rings deposited on their scales, which can be sampled without harm to the animal and which can be read with simple preparation and equipment. American eel scales have annually deposited rings, but the scales first appear when the eels are several years old, which precludes their use as a reliable aging tool (Smith and Saunders 1955). This means that eels must be aged from their otoliths, which requires lethal sampling and specialized expertise and equipment to prepare and read the specimens (ICES 2011).

In contrast, American eel lengths can be obtained rapidly in the field without harm to the animal. Cairns et al. (2007) described a portable system to efficiently measure and weigh eels without anaesthetic (Fig. 15). However, growth rates vary greatly among individual eels and length at age plots form a broad cloud (Fig. 16). Consequently, eel length frequency plots do not show obvious modes that correspond to age cohorts.

Length frequency analysis (LFA) is an analytic technique that decomposes length frequency distributions into age distributions (Hasselblad 1966, MacDonald and Pitcher 1979, MacDonald 1987). LFA, whose origins are in the theory of mixture distributions, is based on the notion that a sequential series of modes in a length frequency dataset may reflect the annual influx of new recruits into the population (Weatherley and Gill 1987). The LFA approach requires a training dataset of ages and lengths, which is used to derive a function that can estimate age structure from samples in which only length has been measured.

In LFA, a length frequency observation was assumed to consist of a fixed number ( $k$ ) of age groups. For each age group  $i=1, 2, \dots, k$ , a random variable of length ( $x$ ) has a definable probability density function (pdf) of  $f_i(x)$ . Therefore, the observed length frequency is a mixture distribution  $g(x|\Theta)$  of  $k$  components of  $f_i(x)$  with mixing weights  $\pi_i$  that can be expressed as:

$$g(x|\Theta) = \pi_1 f_1(x|\theta_1) + \dots + \pi_k f_k(x|\theta_k),$$

where  $\pi_1, \dots, \pi_k$  are mixing weights or proportions ( $0 \leq \pi_i \leq 1$  and  $\sum_{i=1}^k \pi_i = 1; i=1, \dots, k$ );  $\Theta$  and  $\theta$  are parameter vectors for the mixture and component distributions, respectively.

LFA can be performed with the [R package RMIX](#) (MacDonald 1987, 2008; Du 2002), which uses expectation-maximization and Newton-Raphson approaches to compute the maximum likelihood estimation. RMIX also fits a variety of distributions (binomial, Poisson, negative binomial) and provides flexible options on constraints of distribution parameters.

Zhu et al. (2013) applied LFA to measurements of eels ascending the Saunders ladder on the Moses-Saunders Dam. Eels that were measured and aged in 2006-2008 served as a training dataset. Length-only datasets were available for years back to 1975. A 31 day mean passage index was used to scale up age composition estimates to recruits-at-age. From 27 candidate models, the top six models ranked by QAICc weight values were selected to produce multimodal averages with a sum of weight value of 0.96 for length frequency observations from the model validation period. G-statistic analysis indicated that the LFA with multiple model inference approach for the selected models successfully predicted the observed age structure of American eels ( $G_6=4.01, p>0.50$ ) (Fig. 17). For the period 1975-2008, LFA showed age 7 fish with the highest number of recruits (at least 35% higher than any other age group), followed by age 8 fish. During the years of high recruitment (1982-83), about 71% of the recruits were ages

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5-8. The cohorts from the late 1960s through the late 1970s were relative stronger than the rest of time series, exhibiting exponential decline since the late 1970s. However, there seemed to be an improving trend for the cohorts of 1998 to 2004, compared to those of the early 1990s.

American eel lengths-at age were asymmetric, resembling lognormal or Gamma curves (Limpert et al. 2001), suggesting that a few individuals at each age group can likely grow much faster and reach much larger sizes than other eels (Zhu et al. 2013). Such relative rapid growth for a small number of individual eels can skew the length-at-age distribution to the right (long right tail), which amplifies the large variance of length-at-age commonly observed for the species. The rejection of the models with fixed mean configuration for most study years suggests that the mean length at each age varies year by year, but follows the von Bertalanffy growth function for some years. However, the variance of the distribution can be either fixed or modeled by a function of the mean.

A key assumption of LFA is that the training and the length-only datasets have similar growth regimes and similar underlying length-at-age structures. American eel growth rates increase with temperature and decrease with latitude (Jessop 2010, Cairns et al. 2014). In northeastern North America, eels reared in salt and brackish water had growth rates more than double those of eels reared in adjacent fresh water (Cairns et al. 2009, Lamson et al. 2009). For the European eel, Daverat et al. (2012) found that growth varied with temperature, distance from the sea, depth, and salinity. Eel density affects sex ratio (Bevacqua et al. 2019), which in turn affects growth, because male and female eels have different growth schedules (Jessop 2010). Despite firm evidence that American eels in Atlantic drainages of North America form a single genetic stock, eel genotypes vary with the habitat to which they have recruited (Pavey et al. 2015). These genetic differences may produce substantial differences in growth rate (Côté et al. 2015).

With eel growth being influenced by numerous environmental factors, both directly and indirectly through genetic effects, it would seem safest to apply LFA to single areas where environmental factors ought to apply uniformly between training and length-only datasets. A compilation of mean American eel growth rates in the St. Lawrence Basin between the year of recruitment to continental waters and the year of sampling shows approximate stability in growth rates of eels with continental recruitments between the 1960s and the early 2000s (Table 8, Fig. 18). Starting in the middle of the first decade of the 2000s recruitment years, growth rates increased markedly. The training set used by Zhu et al. (2013) was sampled in 2006-2008. With a mean age of about 6 years, these eels would have recruited to continental waters in 2000-2002, prior to the start of the increase in growth rate. This means that, for the Zhu et al. (2013) study, the assumption of similarity in growth rate between training and length-only datasets appears to be satisfied. However, application of the training dataset to subsequent years, where growth rates are higher, would likely lead to erroneous age structure estimates.

The recent increase in American eel growth rates in the St. Lawrence Basin might possibly be a density-dependent effect, because the first cohorts showing higher growth rates would have had their early growth shortly after the near-disappearance of eels in the upper part of the St. Lawrence system, as indicated by research fishing catch per unit effort in waters above the Moses-Saunders dam (Cairns 2020). However, the relation between eel density and growth rate is not clearly established (Boulenger et al. 2016).

Patey et al. (2018) reported an additional example of major changes in eel growth rates in a single location, noting that median lengths of age 1 and 5 European eels in the Gironde Estuary, France, estimated from otolith back-calculation, doubled in the decade between the early 2000s and the early 2010s.

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These findings suggest that LFA might draw erroneous conclusions in cases where the training and the length-only datasets were obtained in different environments. Applications where the two datasets are from the same location should also consider the possibility that temporal changes in growth rates may introduce error in LFA-generated age structures.

### **USE OF LIFE HISTORY PARAMETER CLINES TO FILL GAPS IN STOCK ASSESSMENT INPUT VALUES (CONTRIBUTOR: MARTEN KOOPS)**

Given the variation observed in American eel life history, any range-wide assessment will be challenged to fill data gaps and estimate life history parameters. While a better understanding of American eel life history is needed to develop robust population models, the broad geographic distribution of American eel lends itself to the possibility that data gaps can be filled with functional relationships relating life history traits to environmental or geographic factors (Jessop 2010, Vélez-Espino and Koops 2010). Vélez-Espino and Koops (2010) reviewed American eel life history variation, demonstrating that much of the observed life history variability can be explained by 1) latitudinal productivity gradients, 2) ideal free distribution (IFD) habitat selection, 3) conditional evolutionarily stable strategies (ESS), 4) size at arrival to coastal zones, and 5) temperature variance and annual degree-day effects on somatic growth. This suggests that life history theory and relationships between life history traits and latitude (latitudinal clines) could be used to fill information gaps for a range-wide assessment. Specifically, Vélez-Espino and Koops (2010) suggested the following patterns could bear further evaluation based on observed patterns and life history theory:

- shorter generation times and faster somatic growth at southern latitudes than in northern latitudes;
- shorter generation times and faster somatic growth in coastal-estuarine than in freshwater systems (>50 km inland) in northern latitudes, with an inverse pattern in southern latitudes;
- greater size and age of leptocephali at arrival to the coast at extremes of the geographic range (i.e., distance from spawning grounds) will allow longer inland migrations and a larger proportion of the eel sub-population to exhibit freshwater residency;
- increased body size, longevity, and decreased mortality from south to north;
- increased growth rates from north to south;
- sex ratio bias towards males in productive habitats with lower temperature variance and higher early life somatic growth;
- fecundity as a function of body size, possibly incorporating distance from the spawning grounds.

Jessop (2010) also proposed that latitudinal variability should be examined with respect to life history strategies and theory. Based on compiled data for length, age at maturity, and annual somatic growth rates, Jessop (2010) showed:

- increased length at metamorphosis of female silver eels with latitude and distance from the spawning grounds;
- no size effect for male eels, but mean age at metamorphosis increased with latitude and distance from the spawning grounds;
- annual somatic growth rate decreased with latitude and distance from the spawning grounds for both males and females. Furthermore, somatic growth rates showed a non-linear or piecewise relationship with latitude;

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- adjusting annual somatic growth rates by time spent at suitable temperatures (degree-days  $\geq 10^{\circ}\text{C}$ ) provides a non-linear relationship with latitude, where growth per degree-day increased at latitudes north of  $44.13^{\circ}\text{N}$ .

Jessop (2018) further compiled data on fecundity and ovary maturation from a northern portion of the American eel range (from the St. Lawrence River to Chesapeake Bay). With these data, Jessop (2018) identified a significant overall relationship between fecundity and body size (either length or weight). Geography had a significant but smaller effect, the result being that fecundity increased with both length and distance from the spawning grounds north of Maine.

Finally, Cairns (2020) further reported significant relationships between somatic growth rates and elver length with latitude, and silver eel length and age with distance from the spawning grounds. The existence of data have also been identified that can form the basis for exploring additional latitudinal clines if more data can be found to make these analyses feasible.

While there is potential to explore additional latitudinal clines to inform data-filling needs for a range-wide assessment, these few publications suggest the potential of this approach to estimating the parameters needed when data are limited. Using life history theory and latitudinal clines to fill data gaps and infer life history traits will be associated with greater uncertainty. An additional source of uncertainty arises from the possibility of temporal variation in life history parameters at a single location (q.v. increasing growth rates in St. Lawrence Basin eels, Fig. 18). Such uncertainty would need to be acknowledged in any assessment and could be dealt with through sensitivity analyses, bootstrap techniques, and Monte Carlo simulations (De Leo et al. 2009, Vélez-Espino and Koops 2010, Young and Koops 2014).

## **LIFE CYCLE MODELING (CONTRIBUTOR: MARTEN KOOPS)**

The presumed panmictic nature of the American eel has led to calls for range-wide (or global) models (e.g. De Leo et al. 2009, Vélez-Espino and Koops 2010). Such models would be useful in providing recommendations for strategies to recover and sustainably manage American eel across its range, given the potential implications of actions (or inaction) in one area for conservation objectives in another. Even if a range-wide model could not be parameterized and calibrated sufficiently to set targets (or quotas), the model could be useful as a synthesising framework for improved understanding of American eel population dynamics. Vélez-Espino and Koops (2010) proposed a modeling framework that could serve such a purpose.

To date, no fully range-wide model has been built. Young and Koops (2014) produced a meta-population model of American eel populations in the seven RPA zones between Newfoundland and the US Atlantic Seaboard South (Fig. 1) (this excludes the Northern Atlantic, the Gulf of Mexico, and the Caribbean portion of the species range). Young and Koops (2014) used a matrix approach to model the life cycle of a panmictic population (as proposed by Vélez-Espino and Koops 2010) with a two-sex model to account for sex-based life history differences. Given the scant evidence to support any proposed larval distribution hypothesis, the model was developed to allow a range of maternal effects on larval distribution. The following larval distribution hypotheses were explored and compared:

1. full maternal effect – where larvae distribute exclusively to the maternal zone;
2. full water attraction – where larvae distribute in proportion zonal drainage area with no maternal effect;
3. hybrid maternal effect and water attraction – representing strong maternal effect (0.95) with weak water attraction;

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4. hybrid maternal effect and nearest neighbour – representing strong maternal effect (0.95) with weak straying to adjoining zones.

This model was not calibrated to data, so is entirely a comparison of possible dynamics based on life history and model structure, but it does provide insights into the population dynamics associated with these alternative hypotheses. Young and Koops (2014) found that general patterns in elasticities (a metric of population response to vital rate perturbations), long-term dynamics, and simulated trajectories were generally robust to parameter value uncertainty. However, model output was very sensitive to structural assumptions such as larval distribution. Depending on the larval distribution hypothesis, transient dynamics and population momentum were affected and could produce counterintuitive dynamics such as observed growth in some zones when underlying rates would otherwise suggest stability or decline. These results suggest that it is critical to better understand the mechanisms by which American eel distribute to continental zones, and that future range-wide assessments need to include considerations of population structure, transient dynamics, and population momentum.

## **DISCUSSION**

### **DISTRIBUTION AND ABUNDANCE**

In the data-rich Western Atlantic Region, American eel distributional boundaries are reasonably well known. However, the creation of comprehensive and publically accessible databases of electrofishing and other survey records would enable refinement of these boundaries and accelerate development of population and habitat models.

In the Northern Atlantic Region and the US Gulf of Mexico, exploitation (mining) of extant records would increase the precision of range boundaries, as has been done in Texas ([fishesoftexas.org](http://fishesoftexas.org)). However, in US Gulf of Mexico drainages, eel penetration may be limited by the great length of rivers. Maximum penetration is likely to be mediated by chance, so range boundaries in this area may be poorly-defined and variable, even if good field data are available.

In Mexico and the Caribbean Basin (with the exception of Puerto Rico; Kwak et al. 2019) aquatic monitoring programs are generally not well developed, hence better definition of range boundaries requires new field work, or perhaps renewed data mining efforts following the example of Benchetrit and McCleave (2016).

This report considers three survey methods for eels in lentic (non-flowing) waters, all of which indicate at least relative abundance, and absolute density if some assumptions are met. Because glass bottom boat and electrofishing boat surveys operate at night, both methods are unsuitable for windy conditions for safety reasons. In boat electrofishing, wind ripples reduce ability to see into the water column which is required to dipnet eels. The glass bottom boat is not subject to visibility reduction from wind ripples because observers look through a window which flattens the water. Boat electrofishing produces electric currents that stimulate eels, (presumably) including those that are hidden in the substrate. Glass bottom boat surveys are entirely visual, so any eels that are hidden in the substrate or bottom debris would be undetected. Due to incomplete catchability in the net enclosure method, absolute density is estimated from catch rates using correction factors that have been calculated from removal experiments (Dorow et al. 2019).

In contrast to glass bottom boat and boat electrofishing surveys, field operations of the net enclosure method take place in daytime, which avoids the safety risks that are inherent in nighttime survey work.



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Both the glass bottom boat and boat electrofishing methods require reasonably transparent water, but the net enclosure method has no requirement for water clarity. The glass bottom and net enclosure methods can operate in any salinity, but boat electrofishing, using currently available equipment, requires fresh water. The net enclosure method has been tested in the non-tidal Baltic Sea. In areas with strong tidal currents it is possible that the netting would tend to catch drifting debris, causing it to lean over and alter its ability to retain eels. However, this has not been tested.

The glass bottom boat method compared favourably with traditional capture-mark-recapture surveys in obtaining density estimates with acceptable confidence limits. The capture-mark-recapture method has an additional disadvantage in that sites with low abundance may produce insufficient recaptures to produce valid estimates.

These three methods have the potential to increase the number of available estimates of eel density, which will be of value to stock assessments. However, all of these methods have substantial capital and labour costs. This cost factor will likely constrain their widespread application in the northern, western, and southern parts of the American eel's range.

Because of its relatively low cost, eDNA appears to be the only method considered in this paper that has a practical chance of substantially increasing knowledge of eel distribution in the species' vast northern, western, and southern range. eDNA detects presence, but further research is required to determine to what extent, if any, it has the ability to assay relative or absolute abundance. Glass bottom boat surveys, boat electrofishing, and the net enclosure method may assist in tests of the ability of eDNA to measure eel abundance. eDNA studies can be species-specific, or they can be generic, testing and recording eDNA of all species. It is the latter type of work that will be useful to eel science, because eel science does not have the resources to do eDNA work over large geographic areas. Such studies will be most valuable to eels, and to aquatic science in general, if their findings are posted on public eDNA databases, such as the Aquatic eDNA Atlas (Table 1).

## **ANALYTIC RESOURCES AND TOOLS**

Environmental databases are foundational to many types of freshwater fish habitat modeling. However, there are major gaps in database coverage of electrofishing records, small dams, and dam passability. The large number of uninventoried small dams in the eel's range could have substantial conservation effects, by restricting upstream access, or in some cases, by increasing habitat and allowing access to that habitat.

In the marine environment the recently completed fetch database is the first database to offer high-resolution eel-relevant environmental data over a very large geographic area. However, eel habitat modeling requires multiple input variables. Water depth is a key variable, but the enormous banks of soundings data possessed by hydrographic agencies are generally not available in any ready or standardized form. In the US such data are now becoming accessible through the CoNED program, which generates bathymetric maps that are seamlessly joined to topographic maps (Table 6). In some of the sheltered habitat favoured by eels, official hydrographic charting may be outdated because of sediment movements. Novaczek et al. (2019) used soundings data crowd-sourced from fishing fleets to chart the bathymetry of the Newfoundland Grand Banks at higher resolution than official charts. Application of this approach could lead to up-to-date and high resolution digital bathymetry that could be feedstock to eel models.

This report explored modeling approaches that emphasize glass eel recruitment, the eel life cycle, and GIS-oriented techniques. All of these approaches have substantial data requirements. Because eel length is easy to measure but eel age is hard to measure,

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efficiencies would be achieved if age structure could be calculated from length structure. This method appears to work well as long as the assumption of unchanging growth regime is satisfied. One example for American eels of a growth rate change in the same area was identified. It is not known how frequently this assumption is violated.

The report also looked at the filling in of data gaps in eel demographic parameters by taking advantage of environmental clines in these variables. This approach seems to have some degree of applicability on the Atlantic coast of North America. Filling gaps by interpolation seems reasonably safe. Whether data absences beyond the Atlantic coast of North America can be reliably filled by extrapolation has not been tested.

## **CONCLUDING COMMENTS**

A fisheries stock assessment is essentially the joining of real-world data and analytic tools to produce insight into the status of the stock. This paper reviews novel and underutilized methods and approaches to obtain real-world data, and tools to analyse them. Because of this focus, the paper does not treat "conventional" data-gathering and analytic tools, such as assaying abundance changes by ladder counts or fisheries catch-per-unit effort, and the modeling of current vs. pristine spawner production as used in the European eel stock assessment. Advancement towards a range-wide stock assessment does not imply abandonment of traditional tools, but rather the making available of new options to gather and analyse data.

This paper set out to find and examine ideas that may aid progress to a range-wide assessment for the American eel. Achievement of such an assessment must involve some combination of efficient ways to obtain data in the data-poor part of the species range, and innovative ways to derive insights from data collections that will inevitably be incomplete. This report uncovered no magic ways to do this. The closest it came to is the eDNA technique, which has an easy field collection protocol and is accurate at least as a presence indicator. There is a reasonable prospect that eDNA use will become sufficiently widespread that its findings will clarify eel distribution over broad areas of the US interior, and perhaps the wider Caribbean Basin. This would be a valuable step towards a range-wide assessment.

Most of the other methods and data sources reviewed in this paper are more suited to data-rich parts of the eel's range, because these areas are also rich in resources needed to conduct aquatic science. These methods and data sources are less well suited to data-poor areas, because such areas generally have limited scientific resources. Formidable obstacles remain in the pursuit of a robust range-wide assessment of the American eel.

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## TABLES AND FIGURES

*Table 1. Selected databases that show or potentially show American eel locations.*

Sal. <sup>a</sup>	Location 1	Location 2	Database	Comments	Source
F,S	World	-	Global Biodiversity Information Facility	From professional sources. It also includes those iNaturalist records which are considered to be of research grade. Includes 7,413 American eel records.	<a href="#">Global Biodiversity Information Facility</a>
F,S	US	-	Biodiversity Information Serving our Nation	Contains 11,350 georeferenced records from professional sources. Includes records from GBIF.	<a href="#">Biodiversity Information Serving our Nation</a>
F,S	Atlantic Ocean, inland waters	-	Ocean Biogeographic Information System	From professional sources. Includes 10,746 American eel occurrence records, of which 5,118 are from ocean surveys.	<a href="#">Ocean Biogeographic Information System</a>
F	US	Conterminous states	IchthyMaps	Compiled from fish atlases. Includes 3,241 American eel records.	Frimpong et al. 2016
F,S	World	-	iNaturalist	From citizen science submissions. Includes 503 American eel records.	<a href="#">iNaturalist</a>
F	US	Conterminous states	Aquatic eDNA Atlas	From professional contributors, by crowdsourcing. Includes no American eel records, but the project is rapidly expanding.	<a href="#">Aquatic eDNA Atlas</a>
F	US	TX	Fishes of Texas	From specimen-based occurrence records. Includes 370 American eel records.	<a href="#">Fishes of Texas</a>

<sup>a</sup>Salinity: F, fresh; S, brackish or salt

*Table 2. Marine surveys that may sample American eels but which have not been assembled into multi-survey databases.*

Prov./ state	Survey	References
NL,NS, NB,PE, ME,MA, RI	Cobble-filled bio-collector survey	Hunt et al. 2017
NB,NS, PE	Bay of Chaleur and Northumberland Strait scallop dredge survey	DFO 2019b
NB,NS, PE	Southern Gulf of St. Lawrence glass bottom boat survey	Cairns et al. 2009, Hallett 2013
NS	Beach seine survey of the Atlantic and Fundy coasts of mainland NS	O'Connor 2008
ME	Kennebec and Penobscot Rivers juvenile striped bass and alosine beach seine survey	US Fish & Wildlife Service 2013
NH	New Hampshire estuarine juvenile finfish beach seine survey	US Fish & Wildlife Service 2013
MA	Massachusetts winter flounder beach seine survey	US Fish & Wildlife Service 2013
RI	Rhode Island (Narragansett Bay, Rhode Island Sound, Block Island Sound) seasonal fishery assessment trawl survey	US Fish & Wildlife Service 2013
RI	Rhode Island coastal pond and embayment beach seine survey	US Fish & Wildlife Service 2013
RI	Narragansett Bay and Sakonnet River beach seine survey	US Fish & Wildlife Service 2013
CT	Connecticut winter flounder and small forage fish beach seine survey	US Fish & Wildlife Service 2013
CT	Connecticut and Thames Rivers river herring beach seine survey	US Fish & Wildlife Service 2013
NY	Long Island Sound trap survey	US Fish & Wildlife Service 2013
NY	Hudson Estuary juvenile striped bass beach seine survey	US Fish & Wildlife Service 2013
NY	Hudson Estuary juvenile stripe bass trawl survey	Rago et al. 1995
NY,NJ	Lower Hudson and Raritan Estuary trawl survey	Reid et al. 1999
NJ	Rutgers Great Bay trawl survey	ASMFC 2013a
NJ	PSEG Delaware Bay beach seine survey	PSEG 2009
NJ,PA, DE	Delaware River juvenile striped bass beach seine survey	US Fish & Wildlife Service 2013
DE	Delaware Bay 9.1 m trawl survey	US Fish & Wildlife Service 2013
DE	Indian River and Rehoboth Bay trawl survey	US Fish & Wildlife Service 2013

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Prov./ state	Survey	References
MD	Maryland Atlantic coastal bays trawl survey	Pincin et al. 2014
MD	Maryland Atlantic coastal bays beach seine survey	US Fish & Wildlife Service 2013
MD	Patuxent and Choptank Rivers and Marshyhope Creek juvenile shad beach seine survey	US Fish & Wildlife Service 2013
MD	Choptank River fyke net survey	US Fish & Wildlife Service 2013
MD	Upper Chesapeake Bay winter trawl survey	US Fish & Wildlife Service 2013
MD	Chester River juvenile alosine beach seine survey	US Fish & Wildlife Service 2013
MD	Chester River juvenile alosine trawl survey	US Fish & Wildlife Service 2013
MD	Maryland portion of Chesapeake Bay striped bass beach seine survey	US Fish & Wildlife Service 2013
MD	Maryland Chesapeake Bay 4.9 m trawl survey	US Fish & Wildlife Service 2013
VA	Virginia fresh-oligohaline tidal river boat electrofishing survey	US Fish & Wildlife Service 2013
VA	Virginia fresh-oligohaline tidal river catfish boat electrofishing survey	US Fish & Wildlife Service 2013
VA	Virginia Potomac tributaries northern snakehead boat electrofishing survey	US Fish & Wildlife Service 2013
VA	Virginia lower Chesapeake Bay juvenile striped bass beach seine survey	US Fish & Wildlife Service 2013
VA	Chesapeake Bay multispecies monitoring and assessment trawl survey	US Fish & Wildlife Service 2013
DC	District of Columbia beach seining survey	US Fish & Wildlife Service 2013
DC	District of Columbia nighttime push net survey	US Fish & Wildlife Service 2013
DC	District of Columbia eel pot survey	US Fish & Wildlife Service 2013
NC	Albermarle Sound juvenile striped bass trawl survey	Rago et al. 1995
NC	North Carolina alosine seine survey	ASMFC 2013a
SC	South Carolina estuarine boat electrofishing survey	ASMFC 2013b
GA	Georgia juvenile finfish trawl survey	Georgia Dept. Natural Resources 2008
GA	Georgia St. Simons and St. Andrew beach seine survey	Georgia Dept. Natural Resources 2008
FL to TX	SEAMAP summer and fall Gulf of Mexico shrimp/groundfish trawl survey	Rester et al. 2014, Monk et al. 2015
AL	Alabama Fisheries Assessment and Monitoring Program trawl survey	Valentine et al. 2006
AL	Alabama Fisheries Assessment and Monitoring Program seine survey	Valentine et al. 2006

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*Table 3. American eel estimated densities and confidence intervals from glass bottom boat and capture-mark-recapture surveys in saline and fresh lentic waters of the southern Gulf of St. Lawrence. Data from Cairns et al. 2008, ICES 2009, and Hallett 2013.*

Prov.	Site	Habitat <sup>a</sup>	Method <sup>b</sup>	Date	Duration (d)	Density (eels/ha)		95% CI % dif. from estimate		
						Estimate	Lower 95% CI	Upper 95% CI	Lower	Upper
NB	Pokemouche Estuary	BE	GBB	9 Jun 2008	1	50.5	31.0	72.1	38.6	42.9
NB	Tracadie Bay	BE	GBB	7 Jun 2008	1	62.3	37.7	88.9	39.5	42.7
NB	Tabusintac Estuary	BE	GBB	5 Jun 2008	1	22.0	9.8	37.1	55.4	68.6
NB	Baie Sainte Anne	BE	GBB	4 Jun 2008	1	31.1	18.1	47.1	42.0	51.2
NB	Kouchibouguac Estuary	BE	GBB	10 Jul 2007	1	39.2	10.2	73.1	74.0	86.8
NB	NW Branch Richibucto Estuary	BE	GBB	30 May 2008	1	34.2	16.9	54.3	50.6	58.5
NB	St. Nicholas River, Richibucto	BE	GBB	11 Jul 2007	1	58.3	21.9	101.7	62.4	74.4
NB	Bay du Village, Richibucto	BE	GBB	29 May 2008	1	31.7	16.8	48.9	47.0	54.4
NB	Cocagne Estuary	BE	GBB	24 May 2008	1	17.1	4.7	35.2	72.5	106.2
NB	Shediac Bay	BE	GBB	16 May 2008	1	10.3	0.0	26.1	100.0	153.4
NB	Kinnear Estuary	BE	GBB	17 May 2008	1	19.4	7.7	33.6	60.2	73.7
NS	Pictou Harbour	BE	GBB	12 Jun 2008	1	18.5	4.5	37.5	75.6	103.0
NS	Little Harbour, Pictou County	BE	GBB	14 Jun 2008	1	47.8	26.9	72.0	43.8	50.5
NS	Merigomish Harbour	BE	GBB	11 Jun 2008	1	41.4	26.1	58.1	36.9	40.3
NS	Pomquet Harbour	BE	GBB	4 Jul 2008	1	55.0	36.7	75.2	33.2	36.8
NS	Tracadie Harbour	BE	GBB	2 Jul 2008	1	14.5	2.9	28.8	79.9	99.0
NS	Margaree Estuary	BE	GBB	19 Jul 2007	1	67.2	45.8	90.6	31.9	34.8
NS	Lake Ainslie	L	GBB	18 Jul 2007	1	38.1	9.3	78.2	75.7	105.4
NS	Lake Ainslie	L	GBB	1 Aug 2007	1	41.5	17.6	70.7	57.6	70.4
NS	Lake Ainslie	L	GBB	5 Aug 2007	1	28.3	15.0	43.2	46.8	52.7
NS	Lake Ainslie	L	GBB	6 Aug 2007	1	6.9	0.0	17.2	100.0	151.2
PEI	Mill River Estuary	BE	GBB	14 Jun 2007	1	192.2	82.0	314.0	57.3	63.4

Prov.	Site	Habitat <sup>a</sup>	Method <sup>b</sup>	Date	Duration (d)	Density (eels/ha)		95% CI % dif. from estimate		
						Estimate	Lower 95% CI	Upper 95% CI	Lower	Upper
PEI	Trout River Estuary, Roxbury	BE	GBB	7 Jun 2007	1	74.9	34.2	122.1	54.4	63.2
PEI	Grand River Estuary	BE	GBB	13 May 2007	1	49.0	25.7	76.6	47.6	56.3
PEI	New London Bay	BE	GBB	9 Jun 2007	1	54.5	23.5	90.1	56.9	65.2
PEI	Hope River Estuary	BE	GBB	15 May 2007	1	260.5	159.3	373.1	38.9	43.2
PEI	Murphys Pond, Millvale	FP	GBB	29 May 2007	1	0.0	-	-	-	-
PEI	Clarkes Pond	BP	MR	12 May-15 Jun, 14 Jul-29 Aug 2000	82	24.0	22.1	26.3	7.8	9.6
PEI	Clarkes Pond	BP	MR	13 Jun-7 Aug 2001	56	18.6	11.2	35.7	39.7	92.3
PEI	Lake of Shining Waters	BP	MR	1 Jun-13 Aug 2000	74	20.1	13.6	32.2	32.1	60.2
PEI	Rollings Pond	BP	MR	12 May-15 Jun, 14 Jul-29 Aug 2000	82	251.3	224.1	284.7	10.8	13.3
PEI	Rollings Pond	BP	MR	28 May-7 Aug 2001	72	132.3	69.8	299.0	47.2	126.0
PEI	Hunter River Estuary, Rusticoville	BE	GBB	26 May 2007	1	246.5	158.4	343.4	35.7	39.3
PEI	Bells (Campbells) Pond, Hunter River	FP	GBB	6 Jun 2007	1	370.6	254.9	496.0	31.2	33.8
PEI	Wheatley River Estuary, Cymbria	BE	GBB	25 May 2007	1	124.2	75.1	179.0	39.5	44.2
PEI	Covehead Bay	BE	GBB	27 Jul 2006	1	20.3	0.0	52.1	100.0	156.3
PEI	Covehead Bay	BE	GBB	27 May 2007	1	76.5	37.9	120.9	50.4	58.0
PEI	Cass Pond	FP	GBB	17 May 2006	1	115.0	67.2	168.4	41.6	46.4
PEI	Long Pond, Dalvay	BP	MR	30 May-14 Aug 2000	77	104.9	95.2	116.3	9.2	10.9
PEI	Long Pond, Dalvay	BP	MR	24 Jun-2 Oct 2003	101	138.1	115.3	168.1	16.5	21.7
PEI	Campbells Pond, Dalvay	BP	MR	30 May-14 Aug 2000	77	30.0	24.3	38.1	19.0	27.0
PEI	Campbells Pond, Dalvay	BP	MR	22 Aug-18 Sep 2001	28	15.8	11.8	22.4	25.5	41.1
PEI	Schooner Pond	BP	MR	26 Jun-8 Jul, 20-28 Aug 2000	22	28.1	15.9	59.0	43.4	109.6
PEI	Morell River Estuary	BE	GBB	30 May 2006	1	276.5	193.1	367.5	30.2	32.9
PEI	Morell River Estuary	BE	GBB	1 Jun 2006	1	243.4	150.6	344.2	38.1	41.4
PEI	Morell River Estuary	BE	GBB	14 May 2007	1	701.2	528.6	890.1	24.6	27.0

Prov.	Site	Habitat <sup>a</sup>	Method <sup>b</sup>	Date	Duration (d)	Density (eels/ha)		95% CI % dif. from estimate		
						Estimate	Lower 95% CI	Upper 95% CI	Lower	Upper
PEI	Basin Head	BE	GBB	9 Aug 2005	1	90.0	52.3	132.9	42.0	47.6
PEI	Basin Head	BE	GBB	15 Aug 2005	1	91.0	48.3	140.1	46.9	53.9
PEI	Basin Head	BE	GBB	23 May 2006	1	29.5	9.9	52.2	66.6	76.7
PEI	Flat River Estuary	BE	MR	5 Jul-25 Aug 2002	52	28.3	14.8	64.8	47.7	129.2
PEI	South Pinette Estuary	BE	MR	29 Jul-14 Oct 2000	78	655.8	356.8	1,400.8	45.6	113.6
PEI	North Pinette Estuary	BE	MR	9 Aug-4 Oct 2000	57	171.2	115.4	272.7	32.6	59.3
PEI	North Pinette Pond	FP	MR	13 Sep-22 Oct 2000	40	84.4	38.2	245.2	54.7	190.5

<sup>a</sup>BE: brackish and saltwater bays and estuaries; L: freshwater lakes; BP: coastal barachois ponds, freshwater although sometimes with saltwater intrusion; FP: freshwater ponds formed by dams.

<sup>b</sup>GBB: glass bottom boat surveys, MR: mark-recapture surveys.

**Table 4. Statistical summary of American eel estimated densities and confidence intervals as presented in Table 3.**

Habitat	Parameter	Duration (d)	Density (eels/ha)			95% CI % dif. from estimate	
			Estimate	Lower 95% CI	Upper 95% CI	Lower	Upper
Bays and estuaries	Mean	6.3	114.5	68.1	180.5	51.4	67.1
Bays and estuaries	SD	17.7	160.2	108.3	270.4	18.3	32.8
Bays and estuaries	Min	1	10.3	0.0	26.1	24.6	27.0
Bays and estuaries	Max	78	701.2	528.6	1,400.8	100.0	156.3
Bays and estuaries	N	35	35	35	35	35	35
Freshwater lakes, barachois ponds, and ponds formed by dams	Mean	39.9	80.4	55.9	122.2	36.6	64.6
Freshwater lakes, barachois ponds, and ponds formed by dams	SD	37.2	96.8	74.6	132.7	25.5	54.0
Freshwater lakes, barachois ponds, and ponds formed by dams	Min	1	0.0	0.0	0.0	0.0	0.0
Freshwater lakes, barachois ponds, and ponds formed by dams	Max	101	370.6	254.9	496.0	100.0	190.5
Freshwater lakes, barachois ponds, and ponds formed by dams	N	18	18	17	17	17	17
Freshwater ponds formed by dams (headponds)	Mean	10.8	142.5	90.1	227.4	31.9	67.7
Freshwater ponds formed by dams (headponds)	SD	19.5	159.6	113.3	206.3	23.3	84.2
Freshwater ponds formed by dams (headponds)	Min	1	0.0	0.0	0.0	0.0	0.0
Freshwater ponds formed by dams (headponds)	Max	40	370.6	254.9	496.0	54.7	190.5
Freshwater ponds formed by dams (headponds)	N	4	4	4	4	4	4
From glass bottom boat surveys	Mean	1.0	96.2	59.5	143.5	53.3	65.9
From glass bottom boat surveys	SD	0.0	132.2	98.1	171.7	19.7	33.2
From glass bottom boat surveys	Min	1	0.0	0.0	17.2	24.6	27.0
From glass bottom boat surveys	Max	1	701.2	528.6	890.1	100.0	156.3
From glass bottom boat surveys	N	39	39	38	38	38	38
From mark-recapture surveys	Mean	64.1	121.6	80.6	218.9	30.9	71.7
From mark-recapture surveys	SD	22.5	169.7	100.2	356.3	16.1	55.9

Habitat	Parameter	Duration (d)	Density (eels/ha)			95% CI % dif. from estimate	
			Estimate	Lower 95% CI	Upper 95% CI	Lower	Upper
			From mark-recapture surveys	Min	22	15.8	11.2
From mark-recapture surveys	Max	101	655.8	356.8	1,400.8	54.7	190.5
From mark-recapture surveys	N	14	14	14	14	14	14
All data	Mean	17.7	102.9	65.2	163.8	47.3	67.5
All data	SD	30.3	141.8	98.1	234.3	21.2	40.1
All data	Min	1	0.0	0.0	17.2	7.8	9.6
All data	Max	101	701.2	528.6	1,400.8	100.0	190.5
All data	N	53	53	52	52	52	52



Table 5. Quantitative electrofishing catch at Lake Ontario, Main Duck area (Main Duck and Yorkshire islands) and the upper St. Lawrence River, Mallorytown Flats, from 1984 to 2015, indicating number of eels electrofished per hour that were of natural origin, as well as total catch, including stocked eels. Stocked eels first appeared in these surveys in the upper St. Lawrence River in 2009 and in eastern Lake Ontario in 2010. Mean total length of the catch is provided from 2005 to 2012 for Lake Ontario and 2005 to 2015 for the upper St. Lawrence River. Catch is provided for night electrofishing surveys, except eastern Lake Ontario 1984 to 1996 are day survey results. Results for the day and night surveys are considered to be comparable and reflect eel diel habitat use and activity, which were affected by dreissenid invasion and establishment in 1991-1994. From Casselman and Marcogliese (2014).

Year	Lake Ontario, Main Duck			St. Lawrence River, Mallorytown		
	Natural N·h <sup>-1</sup>	Total		Natural N·h <sup>-1</sup>	Total	
		N·h <sup>-1</sup>	Mean TL (mm)		N·h <sup>-1</sup>	Mean TL (mm)
1984	85.600	85.600	-	-	-	-
1985	63.100	63.100	-	-	-	-
1986	82.900	82.900	-	-	-	-
1987	89.000	89.000	-	-	-	-
1988	68.800	68.800	-	-	-	-
1989	93.000	93.000	-	-	-	-
1990	64.100	64.100	-	-	-	-
1991	38.500	38.500	-	-	-	-
1992	44.400	44.400	-	-	-	-
1993	22.700	22.700	-	-	-	-
1994	30.000	30.000	-	22.250	22.250	-
1995	10.500	10.500	-	-	-	-
1996	14.900	14.900	-	14.300	14.300	-
1997	7.300	7.300	-	-	-	-
1998	12.900	12.900	-	11.030	11.030	-
1999	21.600	21.600	-	14.220	14.220	-
2000	9.370	9.370	-	7.380	7.380	-
2001	6.820	6.820	-	4.730	4.730	-
2002	3.360	3.360	-	2.910	2.910	-
2003	0.650	0.650	-	2.180	2.180	-
2004	0.520	0.520	-	2.010	2.010	-
2005	1.230	1.230	517.3	2.097	2.097	589.0
2006	0.492	0.492	501.3	0.699	0.699	502.4
2007	0.208	0.208	517.4	0.297	0.297	420.2
2008	0.148	0.148	517.4	0 <sup>a</sup>	0 <sup>a</sup>	-
2009	0.192	0.192	536.1	0.184	0.966	421.1
2010	0.000	0.321	521.1	0.000	5.684	425.3
2011	0.000	0.536	514.2	0.000	11.596	422.1
2012	0.000	0.483	540.3	0.000	20.932	423.3
2013	0.277	1.000	-	0.000	14.781	510.0
2014	-	-	-	0.000	12.444	604.0
2015	-	-	-	0.000	6.110	661.6

<sup>a</sup> Eels were not electrofished in the night survey but were in the daytime survey

Table 6. Selected environmental databases that may aid progress towards a range-wide American eel stock assessment.

Theme	Sal. <sup>a</sup>	Location 1	Location 2	Database	Comments	Source
Habitat	F	Canada, US	NS, NB, PE parts of QC, ME, NH, VT, NY	Appalachian-Acadian stream classification	Rivers and streams (but not lakes and ponds), classified by size, gradient, temperature, alkalinity, and tidal influence.	Millar et al. 2019
Habitat	F	US	-	StreamCat, LakeCat	Metrics for 2.6 million stream segments and 378,000 lakes, including flow relations and environmental characteristics.	Hill et al. 2016, US <a href="#">Environmental Protection Agency StreamCat Dataset</a>
Habitat	F	US	Eastern states	Stream classification system	Classification of 92% of eastern US stream reaches based on hydrology, temperature, size, gradient, valley confinement and substrate. Includes a database of ~900,000 fish, mussel, and crayfish records.	McManamay et al. 2018
Habitat	F,S	US	Conterminous states	US National Wetland Inventory	High-resolution GIS maps of wetted habitat in a multi-level classification scheme.	Cowardin et al. 1979, Dahl et al. 2009
Habitat	F	US	Western states	US Forest Service databases	Spatially explicit databases of temperature, stream habitat conditions, fish occurrences, eDNA, and other parameters.	Isaak et al. 2017
Hydrography	F	World	-	Hydrosheds	GIS database of watersheds, river networks, and drainage directions.	<a href="#">WWF HydroSHEDS</a>
Hydrography	F	Canada	-	Canadian National Hydro Network	GIS database of inland water features.	NHN 2012, <a href="#">National Hydro Network – NHN – GeoBase Series</a>
Hydrography	F	US	-	US National Watershed Boundary Dataset	Hierarchical GIS database of watershed boundaries.	USGS and DoA. 2013, <a href="#">National Hydrography Watershed Boundary Dataset</a>

Theme	Sal. <sup>a</sup>	Location 1	Location 2	Database	Comments	Source
Hydrography	F,S	US	Coastal lands and waters from MA to NC, west FL, and AL to east TX	Coastal National Elevation Database (CoNED)	Seamless high-resolution topographic-bathymetric maps in geotiff format.	Danielson et al. 2016, <a href="#">USGS CoNED Viewer</a>
Hydrography	F,S	Canada	-	Canadian Hydrographic Service Non-navigational Bathymetry	Resolution approximately 100 m	<a href="#">Canadian Hydrographic Service Non-navigational Bathymetry</a>
Barriers	F	World	-	Global Dam Watch databases	GRanD, large dams, 6,862 records; GOOD, medium and large dams, from Google Earth records, 38,660 records.	Lehner et al. 2011, <a href="#">Global Dam Watch database</a>
Barriers	F	World	-	Open Street Maps dam database	GIS layer presenting 54,308 OSM features that are tagged as dams. Includes dams of all sizes.	<a href="#">Open Street Maos dam database</a>
Barriers	F	World	-	International Commission on Large Dams	>55,000 records. Accessible for a 230 Euro fee.	<a href="#">International Commission on Large Dams</a>
Barriers	F	Canada	-	Inventory of Large Dams in Canada	1,157 records of dams, generally $\geq 15$ m high or impounding $\geq 3$ million m <sup>3</sup> of water.	Canadian Dam Association 2019
Barriers	F	Canada	Quebec	Dam inventory of the Centre d'expertise hydrique du Québec	Records of 8,398 dams that are 1 m or more in height, with detailed descriptions.	<a href="#">Dam inventory of the Centre d'expertise hydrique du Québec</a>
Barriers	F	US	-	US National Inventory of Dams	91,470 records of dams, generally $\geq 7.6$ m high or impounding $\geq 61,674$ m <sup>3</sup> of water. A derived database (National Anthropogenic Barrier Dataset) is linked to the US National Hydrography Dataset.	Graf 1999, US ACE 2018.

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Theme	Sal. <sup>a</sup>	Location 1	Location 2	Database	Comments	Source
Barriers	F	Canada, US	NS, NB, PE, parts of QC, ME, NH, VT, NY	Appalachian-Acadian Aquatic Connectivity Tool	Stream barriers and potential barriers (dams, n=4,901; waterfalls, n=490; road crossings, n=114,797) and fish records (n=87,855); also a watershed database for Canada based on the same methods as the US National Watershed Boundary Dataset.	Noseworthy et al. 2019
Barriers	F	US	Atlantic states, ME to WV	Freshwater Network Barrier Database	13,889 records of dams and 181,680 other stream crossings. Some dams have detailed ecological metrics. Barriers on small streams that are depicted only at scales below 1:100,000 are not included.	Martin and Levine 2017, <a href="#">Freshwater Network Barrier Database</a>

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Table 7. Number of dams and number and characteristics of water bodies in United States fresh waters.

Inventory name	Region	Number of dams	Water bodies			Proportion that are formed by dams	Criteria for inclusion	Method	Source	Comments
			Number	Area (km <sup>2</sup> )	Type					
National Inventory of Dams	All US	91,468	-	-	-	-	Generally dams $\geq 7.6$ m high or impounding $\geq 61,674$ m <sup>3</sup> of water	Multiple sources including official records and aerial photo interpretation	Graf 1999, US ACE 2018, <a href="https://nid.sec.usace.army.mil/ords/f?p=105:1:.....">https://nid.sec.usace.army.mil/ords/f?p=105:1:.....</a>	-
Freshwater Network Barrier Database	US states, ME to WV	13,889	-	-	-	-	Dams on streams that are depicted at map scales 1:100,000 and coarser	-	Martin and Levine 2017, <a href="https://maps.freshwaternetnetwork.org/north-east/#">https://maps.freshwaternetnetwork.org/north-east/#</a>	-
-	All US	2,000,000	-	-	-	-	Dams impounding $< 61,674$ m <sup>3</sup> of water	-	US ACE unpublished, quoted by Graf 1993	-
-	All US	-	6,570,000	-	Lakes, reservoirs, and ponds	Estimated 2/3	-	From the US National Hydrography Dataset	Renwick 2017	-
-	All US	-	4,000,000 - 4,500,000	-	Water bodies formed by dams	100%	-	From the US National Hydrography Dataset	Renwick 2017	-
-	All US	-	9,000,000	-	Non-riverine water bodies	Most	$> 0.0025$ ha	Extrapolated from 1:24,000 scale maps	Smith et al. 2002	-
-	All US	-	2,600,000	21,000	Non-riverine water bodies	Most	0.06 ha to 1 ha	From satellite images of 30 m pixel size	Smith et al. 2002	-
-	All US in 1934	-	20,000	-	Ponds	-	-	-	Swingle 1970	-
-	All US in 1965	-	$> 2,000,000$	-	Ponds	-	-	-	Swingle 1970	-
-	All US	-	-	21,600	Small ponds	-	-	-	Downing et al. 2006	-
-	Conterminous US	-	2,600,000	-	Small ponds	"overwhelmingly of human origin"	See Method	From satellite images of 30 m pixel size	Renwick et al. 2005	-
-	Conterminous US	-	9,000,000	-	Small ponds	"overwhelmingly of human origin"	See Method	From an extrapolation of counts on 1:24,000 USGS topographic maps, which detect features as small as 5 m across.	Renwick et al. 2005	An estimated 21% of the drainage area of the conterminous US flows through these ponds.
-	Conterminous US	-	4,540,284	30,267	Small ponds	-	Ponds between 0.5 and 40 ha	From the US National Hydrography Dataset, map scale 1:24,000	Fleming and Stubbs 2012	-
-	Atlantic states between ME and FL	-	720,207	6,650	Small ponds	-	Ponds between 0.5 and 40 ha	From the US National Hydrography Dataset, map scale 1:24,000	Fleming and Stubbs 2012	Data also given by state

Inventory name	Region	Water bodies				Proportion that are formed by dams	Criteria for inclusion	Method	Source	Comments
		Number of dams	Number	Area (km <sup>2</sup> )	Type					
National Wetlands Inventory (NWI) <sup>a</sup>	US St. Lawrence Basin	-	-	501	Riverine non-tidal	-	-	Air photo interp.	NWI data (Cowardin et al. 1979, Dahl et al. 2009) as compiled by Cairns et al. 2014	Cairns et al. 2014 also give data by state
NWI	US St. Law. Basin	-	-	2,773	Lacustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US St. Law. Basin	-	-	214	Palustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Scotia-Fundy (Saint John River Basin)	-	-	96	Riverine non-tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US Scotia-Fundy (Saint John River Basin)	-	-	391	Lacustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Scotia-Fundy (Saint John River Basin)	-	-	39	Palustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard N	-	-	175	Riverine tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard N	-	-	598	Riverine non-tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard N	-	-	5,499	Lacustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard N	-	-	796	Palustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard Central	-	-	543	Riverine tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard Central	-	-	753	Riverine non-tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard Central	-	-	939	Lacustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard Central	-	-	623	Palustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard S	-	-	411	Riverine tidal	-	-	Air photo interp.	Ditto	Ditto

Inventory name	Region	Water bodies				Proportion that are formed by dams	Criteria for inclusion	Method	Source	Comments
		Number of dams	Number	Area (km <sup>2</sup> )	Type					
NWI	US Atl. Seaboard S	-	-	781	Riverine non-tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard S	-	-	4,988	Lacustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US Atl. Seaboard S	-	-	1,660	Palustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US all St. Law. and Atl. drainages	-	-	1,129	Riverine tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US all St. Law. and Atl. drainages	-	-	2,728	Riverine non-tidal	-	-	Air photo interp.	Ditto	Ditto
NWI	US all St. Law. and Atl. drainages	-	-	14,590	Lacustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US all St. Law. and Atl. drainages	-	-	3,330	Palustrine	-	-	Air photo interp.	Ditto	Ditto
NWI	US all St. Law. and Atl. drainages	-	-	21,777	All freshwater habitat	-	-	Air photo interp.	Ditto	Ditto

<sup>a</sup>All NWI data shown in this table are for freshwater non-emergent aquatic habitat. Non-emergent aquatic habitat is habitat which lacks rooted plants that have stems and leaves extending above the water surface.

*Table 8. Mean lengths, mean ages, and mean growth rates between recruitment to continental waters and year of sampling of American eels in the St. Lawrence Basin.*

Sampling year	Sampling location	Stage	Origin	Length (mm)			Age			Recruitment year	Mean Growth (mm/yr) <sup>a</sup>	Source
				Mean	SD	N	Mean	SD	N			
1970	St. Lawrence Estuary between Nicolet and Cacouna	Silver	Natural	792.0	-	3,841	16.8	-	-	1953	43.3	Larouche et al. 1974
1975	Saunders ladder	Yellow	Natural	332.0	-	533	6.0	1.7	533	1969	44.8	Liew 1976
1993	Saunders ladder	Yellow	Natural	493.0	-	65	11.9	-	-	1981	36.1	Casselma et al. 1997, Casselma 2003
1990s	Upper St. Lawrence/ Lake Ontario	Yellow	Natural	838.0	24.0	-	17.8	0.9	-	1977	43.5	Casselma et al. 1997, Casselma 2003
1990s	Saunders ladder	Yellow	Natural	493.0	17.0	-	11.9	1.1	-	1983	36.1	Casselma 2003
2001	Kamouraska, St. Lawrence Estuary	Silver	Natural	837.0	69.0	30	20.1	4.0	30	1981	38.5	Tremblay 2009
2002	Upper St. Lawrence River, near the Iroquois Dam	Silver	Natural	1,001.0	66.0	30	21.0	4.0	30	1981	44.7	Tremblay 2009
2004	Beauharnois ladder	Yellow	Natural	420.2	129.0	88	6.3	2.2	82	1998	56.8	Verreault and Tardif 2006
2006	Saunders and Moses ladders	Yellow	Natural	354.0	52.0	44	6.6	1.6	44	1999	44.0	K.Oliveira unpubl. in Cairns et al. 2008
2008	Saunders ladder	Yellow	Natural	367.6	74.0	102	5.5	1.5	88	2003	55.8	D. Stanley, Ontario Power Generation, unpubl.
2009	Beauharnois ladders	Yellow	Natural	322.9	63.3	3,858	4.1	1.8	76	2005	63.3	Verreault et al. 2014
2010	Saunders ladder	Yellow	Natural	360.2	67.3	111	4.9	1.5	113	2005	60.4	Stacey et al. 2015



Sampling year	Sampling location	Stage	Origin	Length (mm)			Age			Recruitment year	Mean Growth (mm/yr) <sup>a</sup>	Source
				Mean	SD	N	Mean	SD	N			
2011	Saunders ladder	Yellow	Natural	371.9	57.5	95	4.6	1.5	99	2006	66.7	D. Stanley, Ontario Power Generation, unpubl.
2011	Beauharnois ladders	Yellow	Natural <sup>b</sup>	344.6	70.1	5,185	4.4	1.6	78	2007	63.9	Verreault et al. 2014
2012	Saunders ladder	Yellow	Natural	340.9	40.9	50	4.2	1.3	50	2008	65.8	D. Stanley, Ontario Power Generation, unpubl.
2013	Saunders ladder	Yellow	Natural	360.8	63.0	48	6.0	2.1	49	2007	49.3	D. Stanley, Ontario Power Generation, unpubl.
2013	Beauharnois ladders	Yellow	Natural <sup>c</sup>	369.1	72.6	4,909	4.8	1.3	73	2008	63.7	Verreault et al. 2014
2014	Saunders ladder	Yellow	Natural	362.6	46.4	29	6.5	1.9	29	2007	45.9	D. Stanley, Ontario Power Generation, unpubl.
2015	Saunders ladder	Yellow	Natural	405.8	67.1	101	5.3	1.2	101	2010	64.4	D. Stanley, Ontario Power Generation, unpubl.
2016	Saunders ladder	Yellow	Natural	391.1	60.3	102	5.2	1.6	92	2011	63.0	D. Stanley, Ontario Power Generation, unpubl.
2017	St. Lawrence Estuary near Kamouraska	Silver	Stocked	792.8	113.4	56	9.9	1.4	56	2007	73.7	Verreault and Dussureault 2018a
2017	St. Lawrence Estuary near Kamouraska	Silver	Natural	904.1	84.4	111	12.5	2.6	106	2004	67.3	Verreault and Dussureault 2018a
2018	St. Lawrence Estuary near Kamouraska	Silver	Stocked	809.7	116.7	95	10.9	1.2	95	2007	68.5	Verreault and Dussureault 2018b

Sampling year	Sampling location	Stage	Origin	Length (mm)			Age			Recruitment year	Mean Growth (mm/yr) <sup>a</sup>	Source
				Mean	SD	N	Mean	SD	N			
2018	St. Lawrence Estuary near Kamouraska	Silver	Natural	905.3	87.9	219	13.6	3.2	219	2004	61.9	Verreault and Dussureault 2018b
2017	Saunders ladder	Yellow	Natural	427.0	78.7	104	5.2	1.5	104	2012	70.1	D. Stanley, Ontario Power Generation, unpubl.
2018	Saunders ladder	Yellow	Natural	398.6	69.9	1,071	6.2	1.3	1,066	2012	54.1	D. Stanley, Ontario Power Generation, unpubl.
2011-2012	Lake St. Francis	Yellow	Natural	439.0	-	26	5		5	2007	75.1	Patey et al. 2018
2011-2012	Lake St. Pierre	Yellow	Natural	457.0	-	21	5		5	2007	78.7	Patey et al. 2018

<sup>a</sup>Growth rate is computed using a length at recruitment of 63.3 mm, which is the mean of the mean length of elver samples from Rivière Blanche (60.0, 67.1; compilation of Jessop 2010) and from Grande Rivière Blanche (62.9, compilation of Côté et al. 2013).

<sup>b</sup>The sample of aged eels includes 2 eels, ages 5 and 6 years, which were identified as stocked by the presence of otolith oxytetracycline marks.

<sup>c</sup>The sample of aged eels includes 1 eel, age 3 years, which was identified as stocked by the presence of otolith oxytetracycline marks.

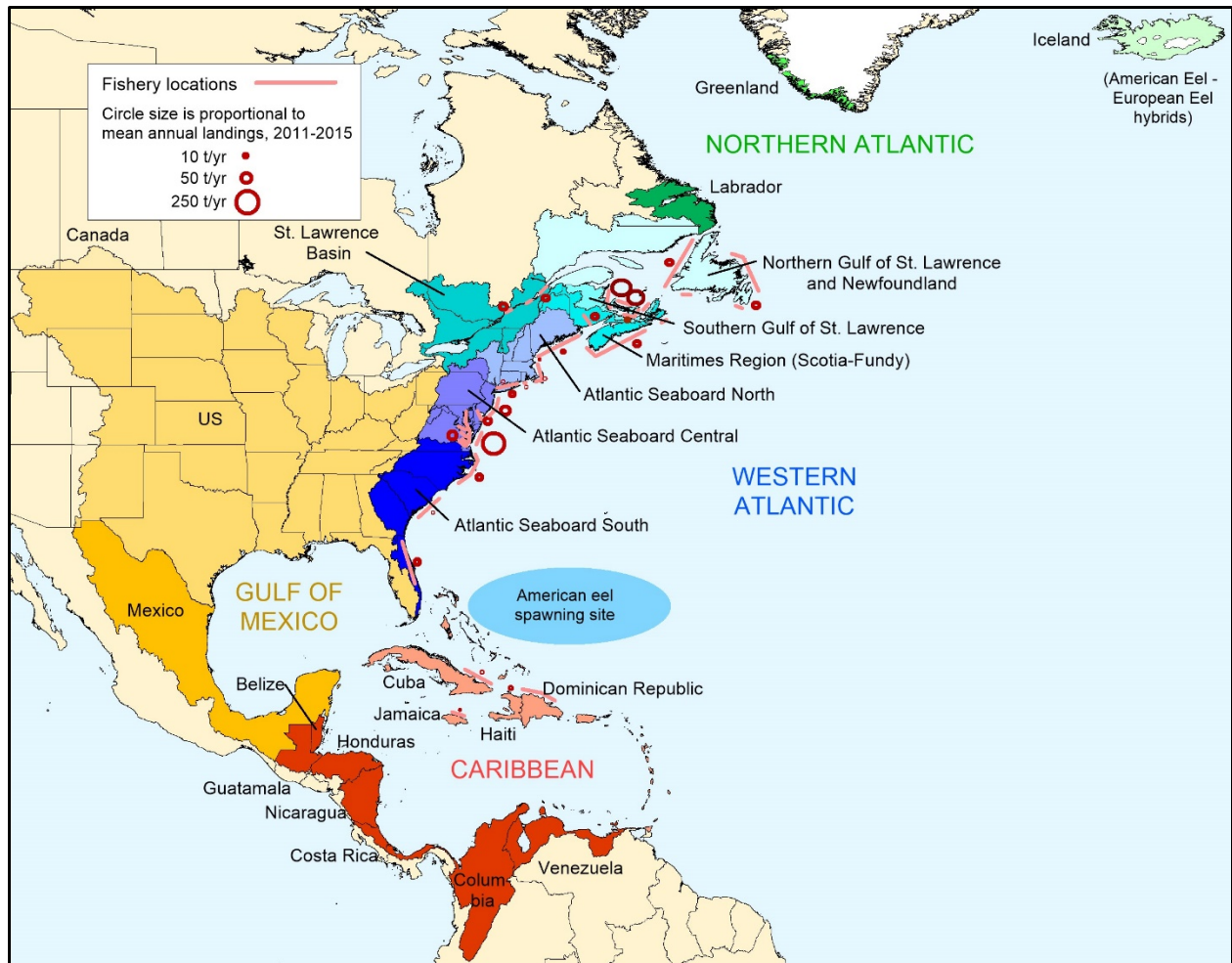
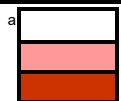

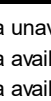


Fig. 1. Fishery locations and plausible native continental range of the American eel, indicated by green (Northern Atlantic Region), blue and purple (Western Atlantic region), brown and amber (Gulf of Mexico Region), and red and pink (Caribbean Region). Colour shades within the Western Atlantic Region indicate Recovery Potential Assessment (RPA) Zones. Actual American eel continental range is a subset of the mapped plausible range. The American eel spawning site is from Miller et al. (2015).

Parameter	Data availability in: <sup>a</sup>												
	Ice-land	Green-land	Lab-rador	Nfld, N. Gulf of St. Law.	St. Basin of Law.	S. Gulf of St. Law.	Mari-times Re-gion	US North	Atlantic Central	Seaboard South	US Gulf of Mex.	Mex-ico	Carib-bean
Elver length													
Growth rate	Fresh female												
	Fresh male												
	Saline female												
	Saline male												
Silver eel length	Fresh female												
	Fresh male												
	Saline female												
	Saline male												
Silver eel age	Fresh female												
	Fresh male												
	Saline female												
	Saline male												
Sex ratio	Fresh												
	Saline												
Fecundity	Fresh												
	Saline												
Natural mortality	Fresh												
	Saline												
Density	Fresh												
	Saline												
Genotype <sup>b</sup>													

<sup>a</sup>  Data unavailable  
 Data available from statistically significant regressions of life history parameter clines  
 Data available from local measurements

<sup>b</sup>Genotype measured for the purpose of evaluating the panmixia hypothesis

Fig. 2. Geographic availability of data on American eel elver length, eel growth, silver eel length, silver eel age, sex ratio, fecundity, natural mortality, and density by region, salinity, and sex. Based on compilations in Cairns 2020.

Approach	Application of the approach to this region is: <sup>a</sup>												
	Green-land	Lab-rador	Nfld, N. Gulf of St. Law.	N. St. Basin of Law.	S. Gulf of St. Law.	Mari-times Region	US N. Seaboard	Atlantic Cent. S.	US Gulf of Mex.	Mex-ico	Carib-bean	Open ocean	
<b>Distribution and abundance</b>													
Mining of range records	E	E	E	E	E	E	E	E	E	E	E	E	E
Abundance from glass bottom boat surveys	F	F	F	F	F	F	F	F	F	F	F	F	F
Abundance from boat electrofishing	F	F	F	F	F	F	F	F	F	F	F	F	F
Abundance from net enclosures	F	F	F	F	F	F	F	F	F	F	F	F	F
Distribution and abundance from environmental DNA	F	F	F	F	F	F	F	F	F	F	F	F	F
Abundance from larval surveys													F
<b>Analytic resources and tools</b>													
Environmental databases	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A
Fetch as a covariate of abundance	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A	E,F,A
Accounting for net effects of small dams	F,A	F,A	F,A	F,A	F,A	F,A	F,A	F,A	F,A	F,A	F,A	F,A	F,A
Development of a pilot GIS-based habitat model	F,A	F,A	A	A	A	A	A	A	A	F,A	F,A	F,A	F,A
Spatio-temporal New Zealand model	F,A	F,A	A	A	A	A	A	A	A	F,A	F,A	F,A	F,A
Glass eel recruitment as an assessment foundation	F	F	F		F	E	E	E	E	F	F	F	F
Estimating age structure from length structure	F	F	E	E	E	E	E	E	E	F	F	F	F
Use of life history parameter clines to fill gaps in stock assessment input values	F	F	E	E	E	E	E	E	E	F	F	F	F
Life cycle modelling	F	F	E	E	E	E	E	E	E	F	F	F	F

<sup>a</sup>Key: Application is:

- Not feasible
- Feasible but not yet applied
- Feasible, has been applied to some extent
- Feasible, has been applied to a substantial extent

Data for further development: E - Extant, F - requires new field work, A - requires new analysis

Fig. 3. Main features of methods and data sources treated in this paper.

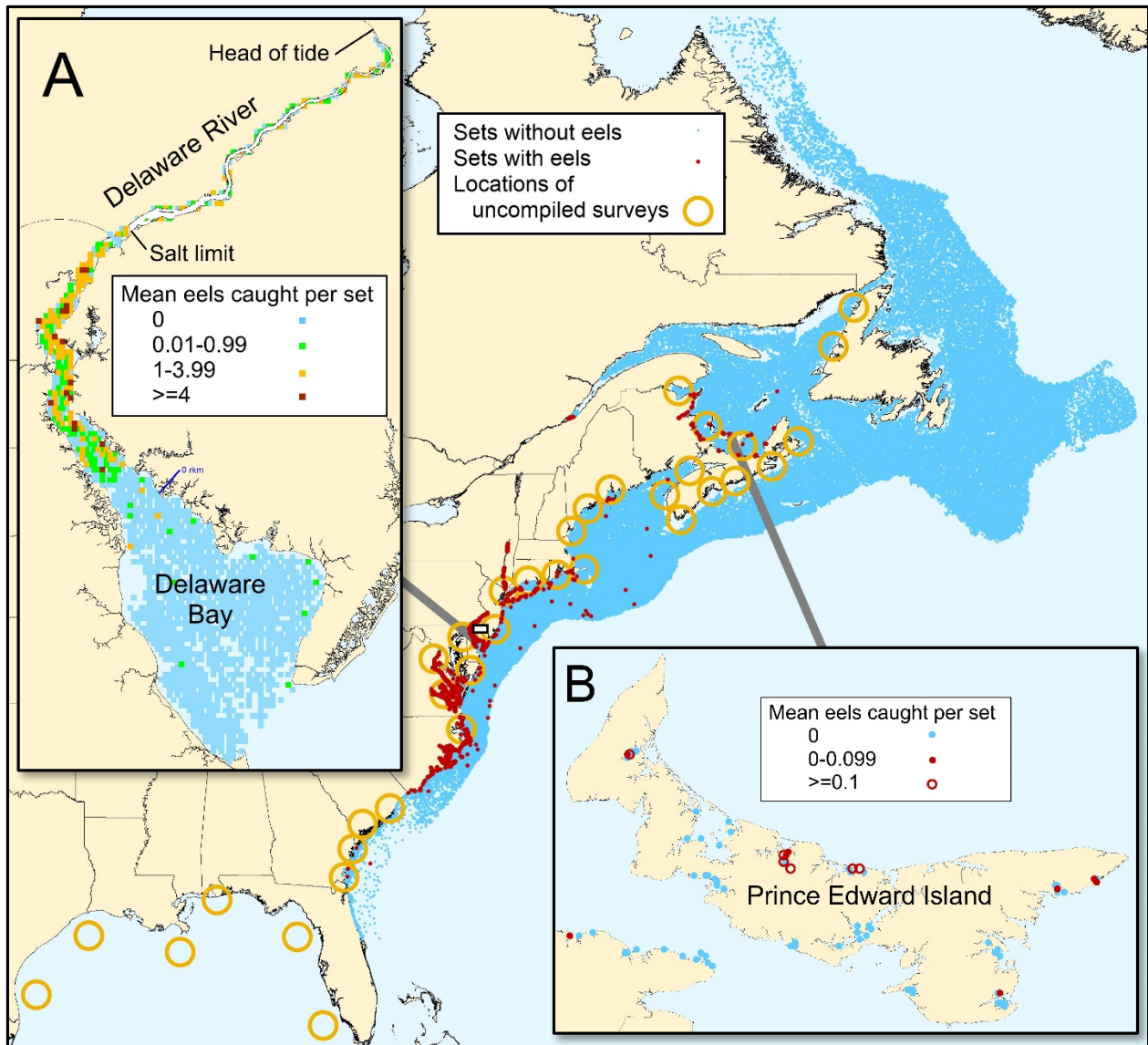


Fig. 4. Locations of 248,769 sets from 26 bottom trawl and beach seine surveys on the east coast of North America, of which 10,715 reported American eels, as compiled by Cairns et al. (2017). Approximate locations of surveys that have not been compiled in multi-survey databases are also shown. Inset A: Eel catch rate in the PSEG bottom trawl survey in Delaware River and Bay. Inset B: Eel catch rate in Community Aquatic Monitoring Program beach seines in Prince Edward Island.

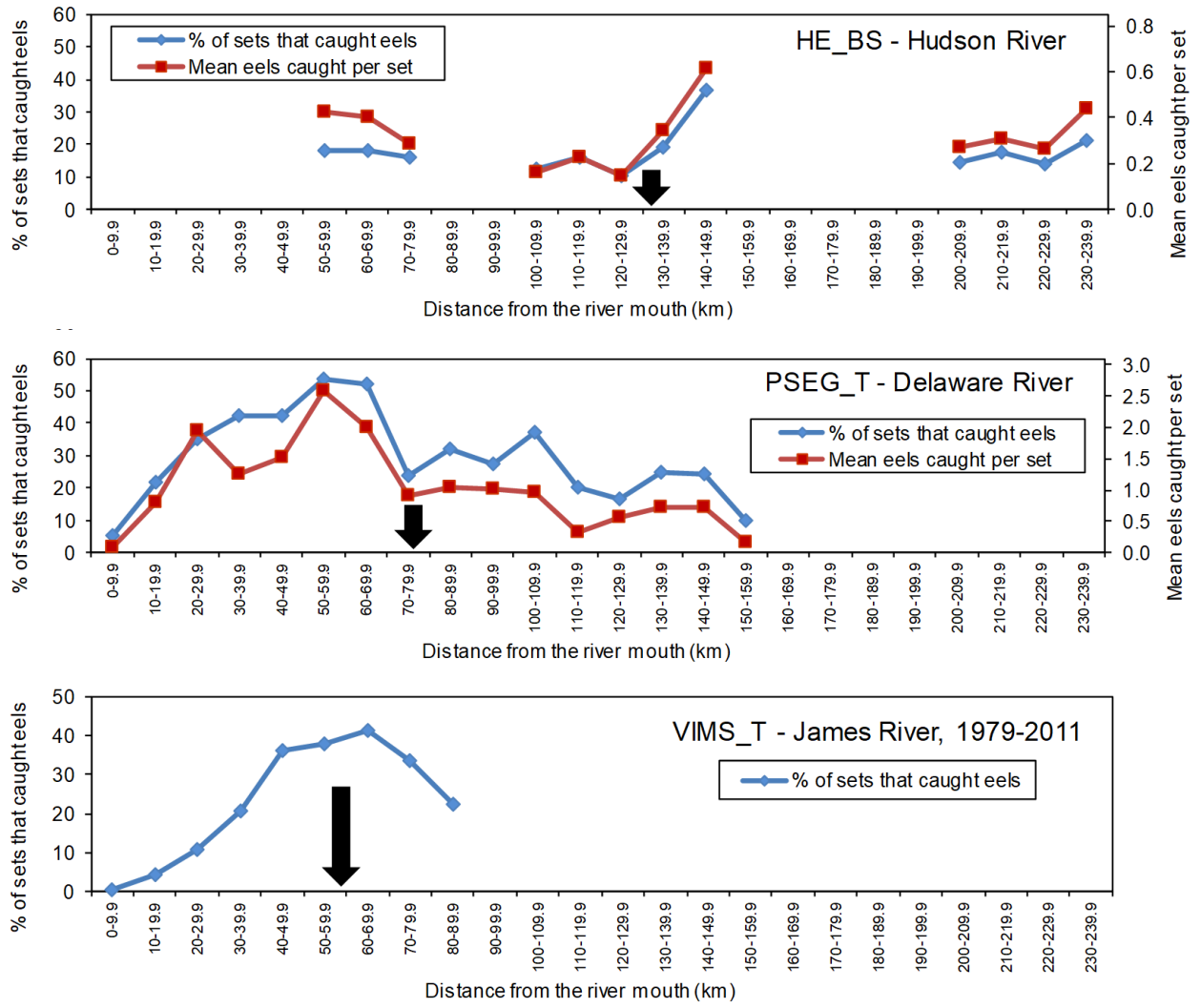


Fig. 5. American eel catch rates with respect to distance from the mouths of the Hudson, Delaware, and James River estuaries, from surveys compiled by Cairns et al. (2017). Black arrows indicate the boundary between the saline and fresh estuaries.



Fig. 6. Location of American eel records for Central America as assembled by Benchetrit and McCleave (2016).



**RETURN showing the Number, Tonnage and Value of Vessels and Boats engaged in the Fisheries: Quantity and Value of Fishing Material; Kinds and Quantities of Fish, and the Total Number of Men employed, &c., in the Province of Nova Scotia, for the Year 1876.**

COUNTIES.	KINDS OF FISH.														VALUE.	WHERE MARKED.			
	Alewives, barrels.	Cod, cwt.	Cod Tongues and Sounds, barrels.	Pollack, cwt.	Hake, cwt.	Haddock, lbs.	Halibut, lbs.	Shad, barrels.	Bas, lbs.	Trout, lbs.	Smelt, lbs.	Eels, barrels.	Oysters, barrels.	Lobsters, cans, lbs.			Fish Oil, gallons.	Fish Guano, tons.	Fish used as manure, barrels.
<i>Halifax.</i>																			
1 North Shore.....	50	1000	5												300			32,555 00	Halifax.
2 French Village.....		2640	13			200000						30			792			80,625 80	do
3 Peggy's Cove.....		300	2			300000						20		500000	90			20,627 50	do
4 Dover.....	30	1500	8			300000	5000					50			450			49,528 50	do
5 Prospect.....		2500	13		100	10000							10000		730			54,028 50	do
6 Terrence Bay.....		1300	7		100	15000									330			30,052 50	do
7 Pennant.....	100	800	4												240			8,284 00	do
8 Sambro.....		3450	17		100	20000	5000							100000	1020			38,882 00	do
9 Ketch Harbour.....	30	4000	20			10000	35000								1200			25,525 00	do
10 Portuguese Cove.....		300	2		100	18000									90			7,702 50	do
11 Herring Cove.....		4000	20		260	45000	100000								1200			38,170 00	do
12 Ferguson's Cove.....		1500	8		50		50000								450			24,323 50	do
																		20,000 00	do
13 Ecum Secum to Beaver Harbour.....		1805			13	46032			1280	700	25	272184		892		50		57,686 62	do
14 Sober Island to Murhatoon.....	42	635				43456			1450	1100	1	114000		347		60		32,333 41	do
15 Spry Bay to Pope's Harbour.....		4198	4		38	17136			1050	20100	35			2740				61,074 66	
16 Tangier to Ship Harbour.....	103	2298			50	39872	1600		750	540	6			1336				22,595 63	
17 West side of Ship Harbour to Clam Bay.....	11	1529			5	2016	500		950	1100	3	72000		773		45		34,560 91	
18 East and West Jeddore.....	40	5031	3	4		84272			1050	2500	20	38688		2680				41,675 12	
19 Musquodoboit to East side of Chezzetcook.....	110	3371				32032			5000	2800	110	102048		1824				42,716 92	

Fig. 7. Reported fishery landings by species and by section of the coast in Halifax County, Nova Scotia, 1876. From Supplement No. 4 to the Ninth Annual Report of the Minister of Marine and Fisheries, from publications.gc.ca.

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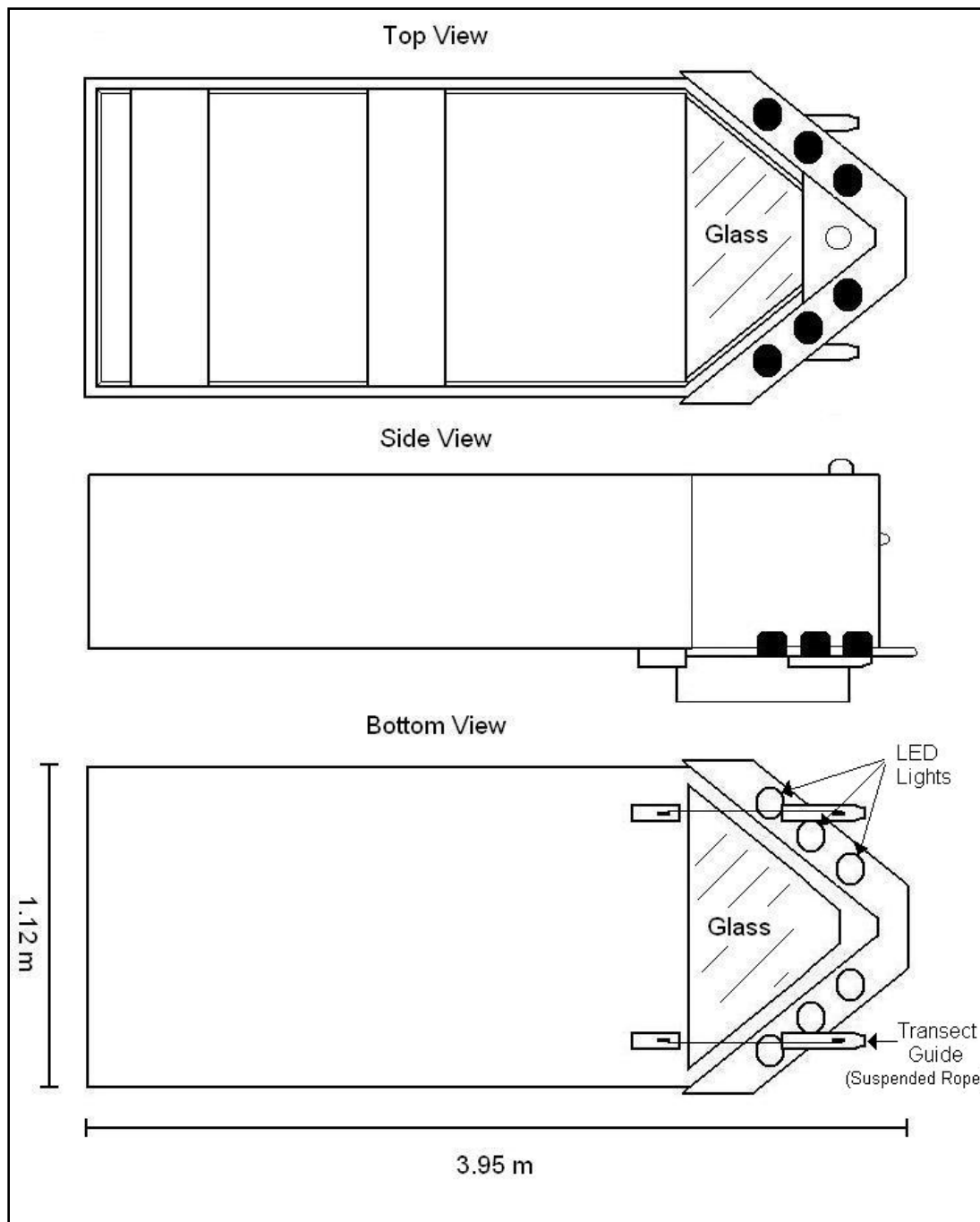


Fig. 8. Schematic diagram of the glass-bottom boat used by Cairns et al. (2009) and Hallett (2013).



*Fig. 9. Quantitative daytime eel electrofishing at A) Main Duck Island, eastern Lake Ontario, and B) the mouth of Jones Creek in the upper St. Lawrence River.*

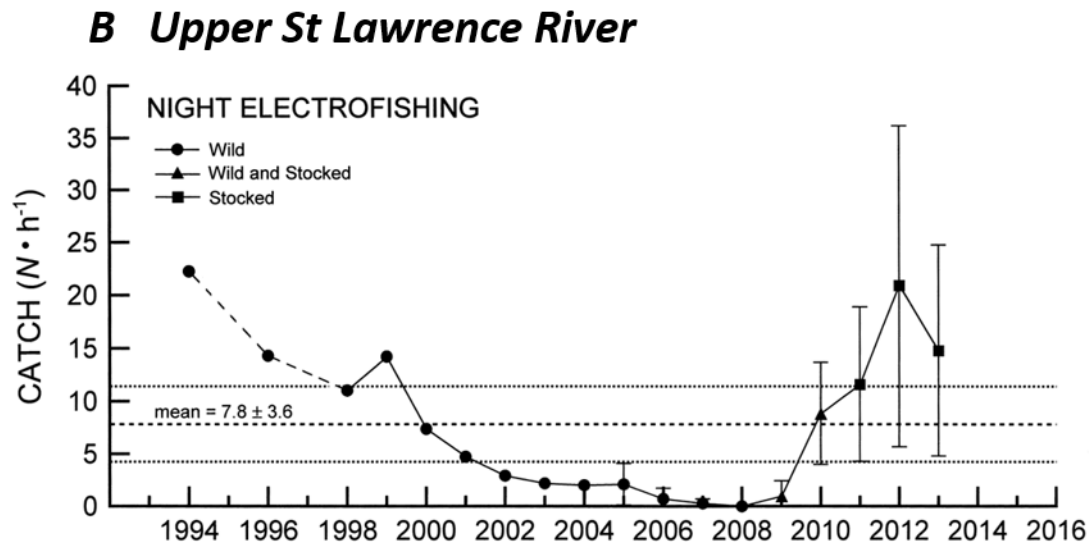
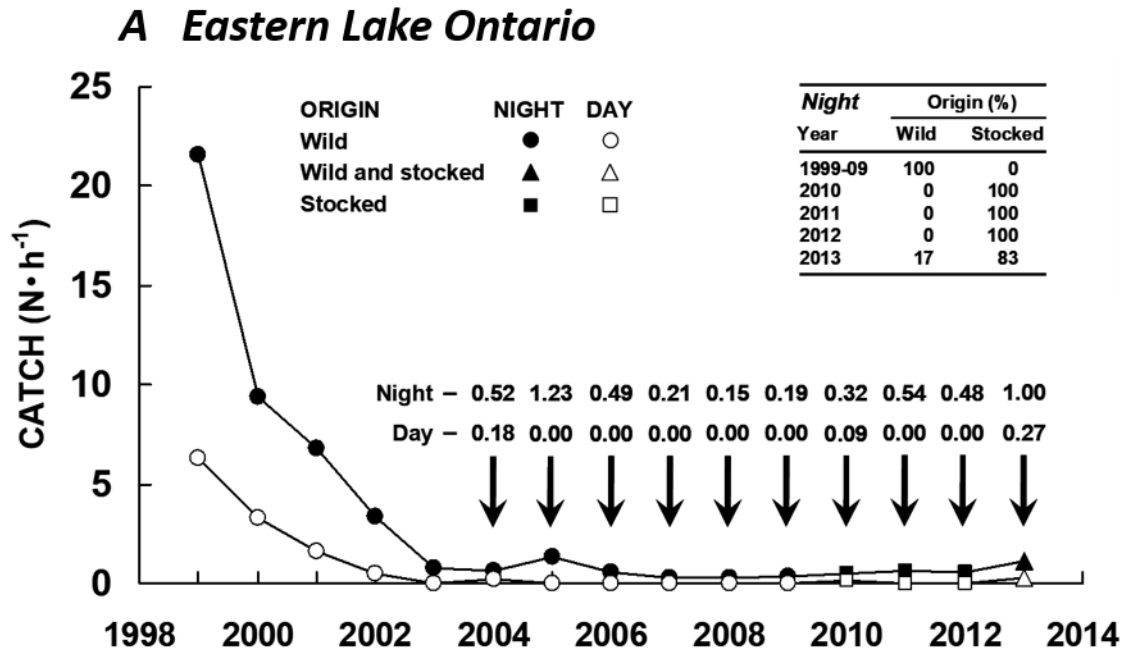


Fig. 10. Boat electrofishing catch ( $N$ ) of eels per hour in eastern Ontario surveys. A) Eastern Lake Ontario at Main Duck and Yorkshire islands from 1999 to 2013 in 36 transects during daytime (open symbols) and nighttime (closed symbols) for natural and stocked eels, determined by necropsy. Numbers are provided, along with a table (inset) describing stock origin. B) Upper St. Lawrence River in the Mallorytown area from 1994 to 2013 in 23 nighttime transects; symbols indicate eel origin determined by necropsy; 95% confidence limits provided. From Casselman and Marcogliese unpubl.

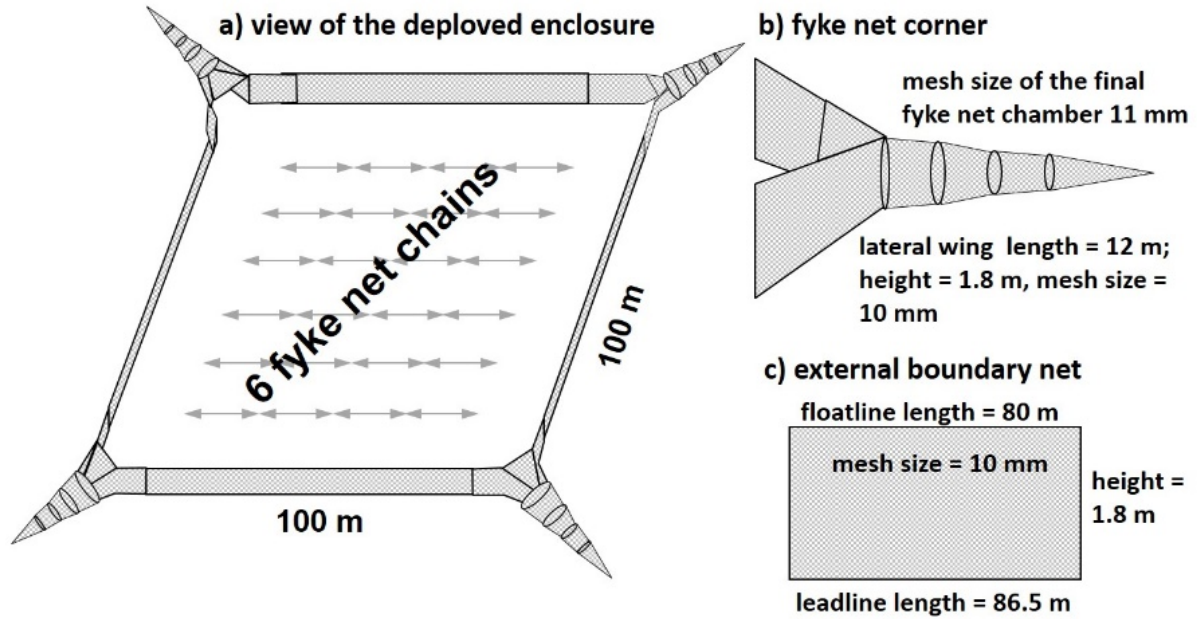


Fig. 11. Schematic view of the net enclosure system. The external boundary net encloses a square area of 1 ha. Eels are captured by fyke nets set at the corners and in chains in the interior (adapted from Ubl and Dorow 2015).



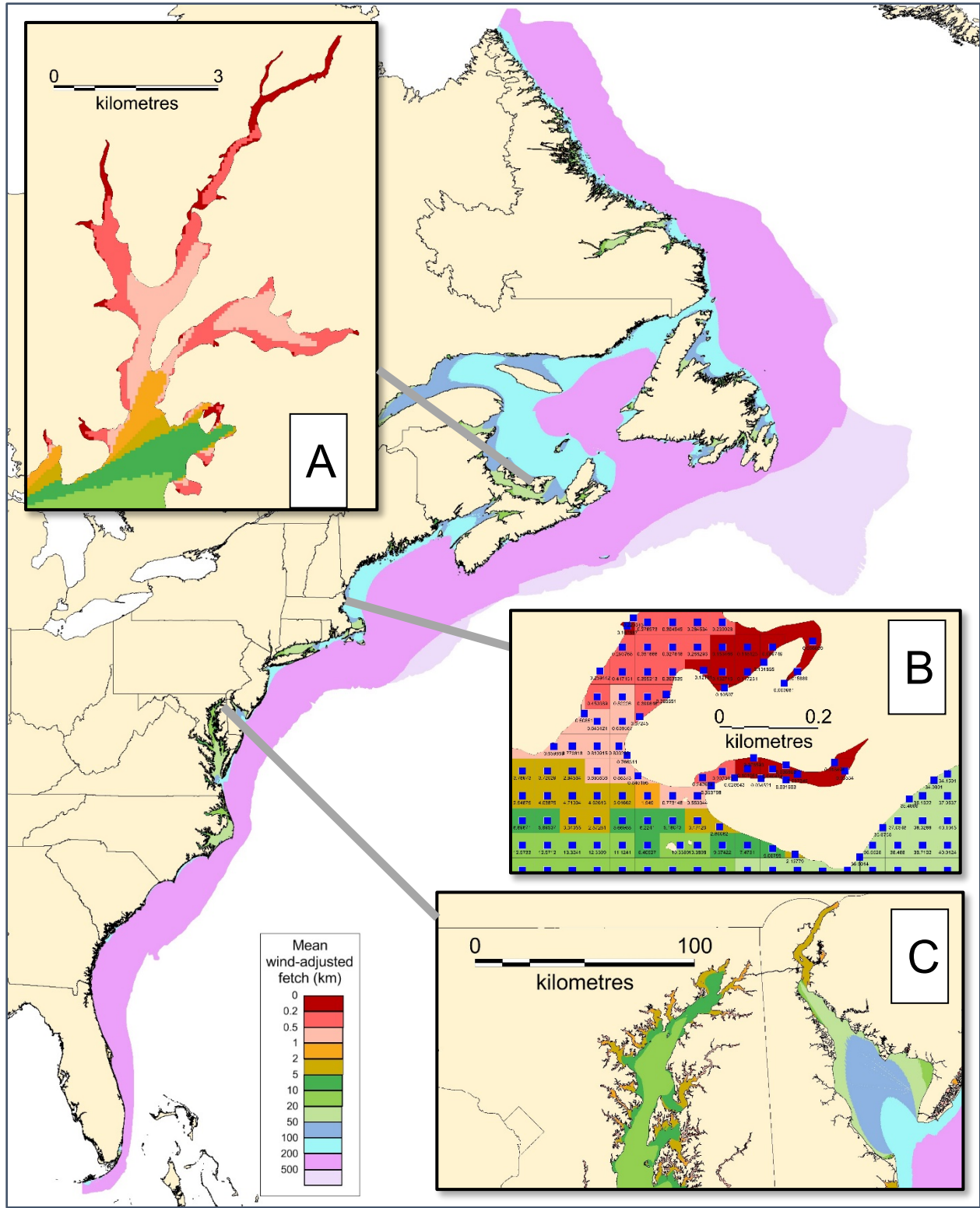
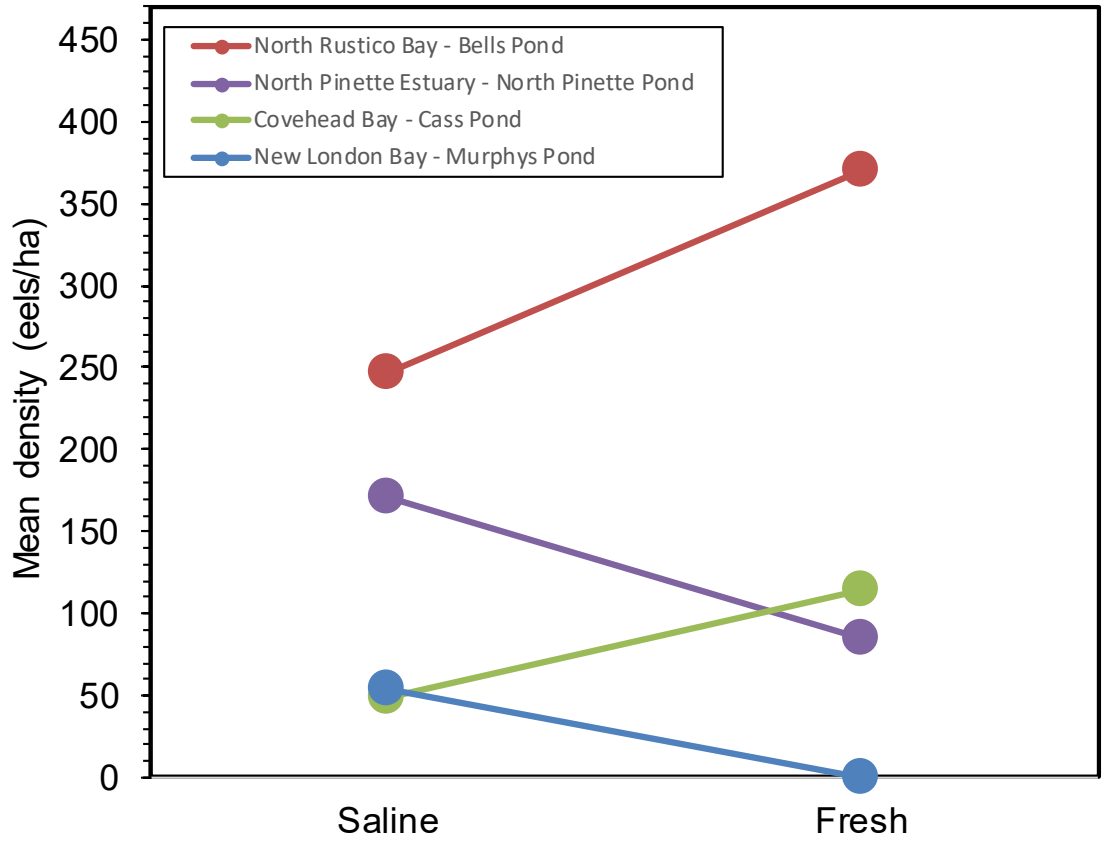


Fig. 12. A map of mean wind-adjusted fetch on the east coast of North America, to the 500 m contour, based on 50 m x 50 m cells up to 5 km from the coast and 200 m x 200 m cells beyond. Inset A: Seal, Vernon, and Orwell Rivers, Prince Edward Island. Inset B: Salisbury, Massachusetts, showing 50 m 50 m Voroni cells, their centroids, and numerical fetch values. Inset C: Northern Chesapeake and Delaware Bays. From D.K Cairns and D.E. Mills unpubl.



*Fig. 13. Mean densities of American eels estimated by capture-mark-recapture and glass bottom boat surveys in saline bays and estuaries and adjacent freshwater impoundments on Prince Edward Island.*

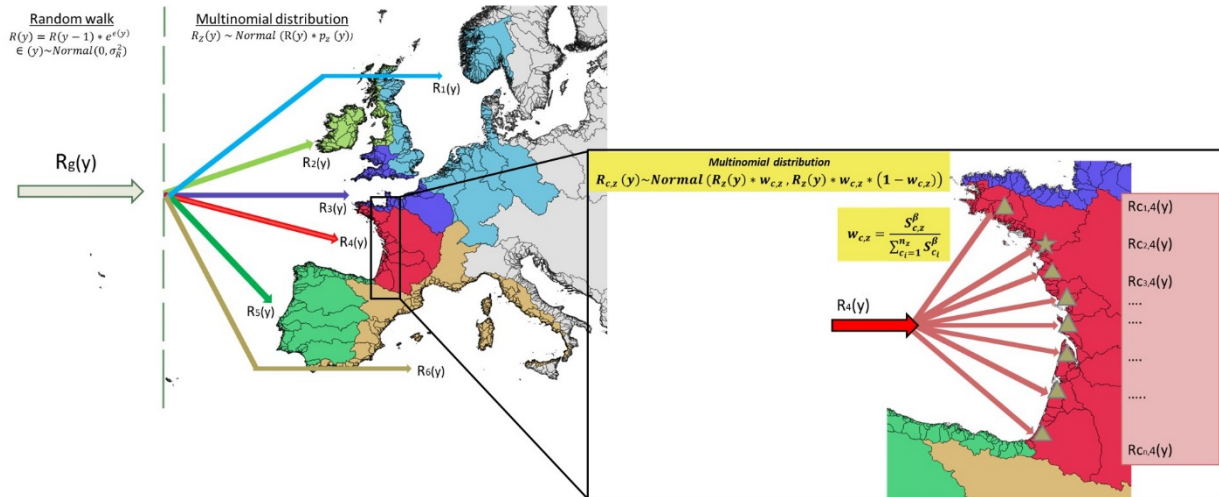


Fig. 14. Summary of the application of GEREM to the European eel. The overall recruitment is assumed to follow a random walk and it is divided into recruitment zones with proportions per zone ( $p_z$ ) varying over years. Zonal recruitment is then split into river catchments according to marginal normal distributions. The weight ( $w_{c,z}$ ) of each catchment is calculated as a power function of its surface area to reflect certain catchment attributes such as river discharge. This last assumption implies that 1) catchment recruitments within a zone must follow a similar trend ( $w_{c,z}$  constant over time), 2) catchment recruitments within a zone must have similar densities, and 3) at least one time-series or point estimate of absolute recruitment is available per zone.





*Fig. 15. A system for efficient eel measuring and weighing. An eel from the tilting intake bin is poured into the measuring trough, where its length is measured against an embedded metre stick. When the spring-loaded trap door is pulled open, the eel falls into the pan where it is weighed. The legs are detachable from the trough for transport and storage. The inset shows how the intake bin is mounted on brackets that are attached to the legs.*

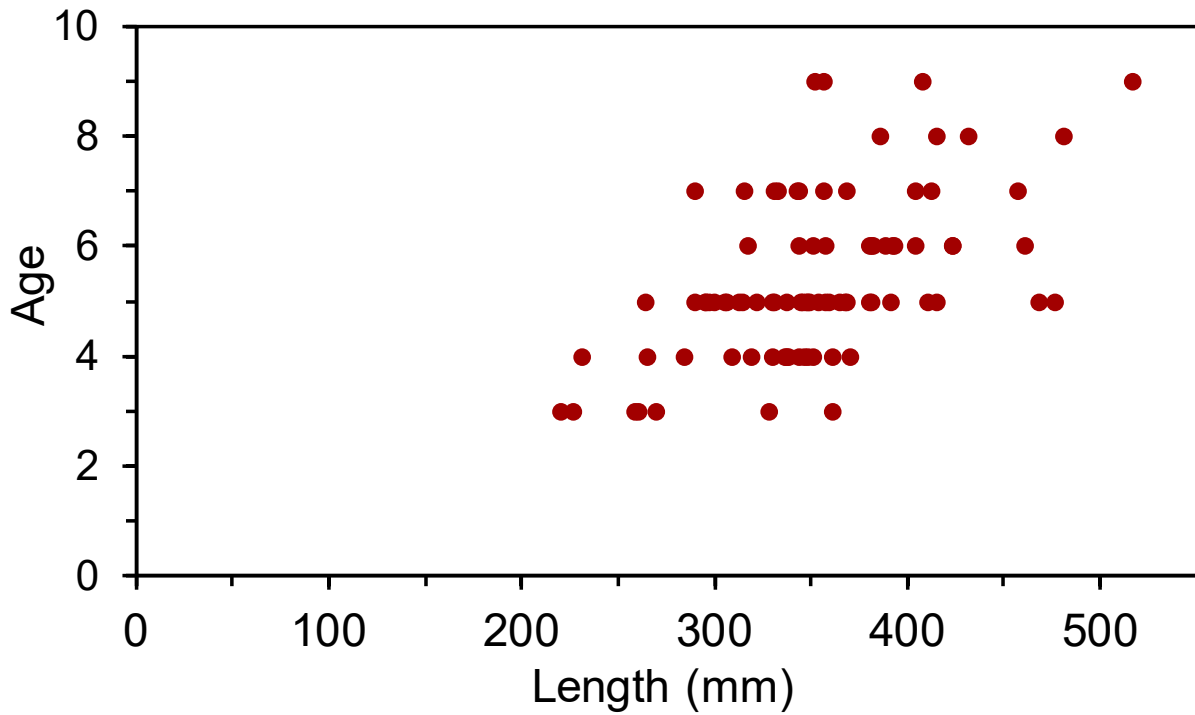


Fig. 16. Length at age of American eels sampled from the Saunders ladder of the Moses-Saunders Dam in 2018. Data courtesy of D. Stanley, Ontario Power Generation.

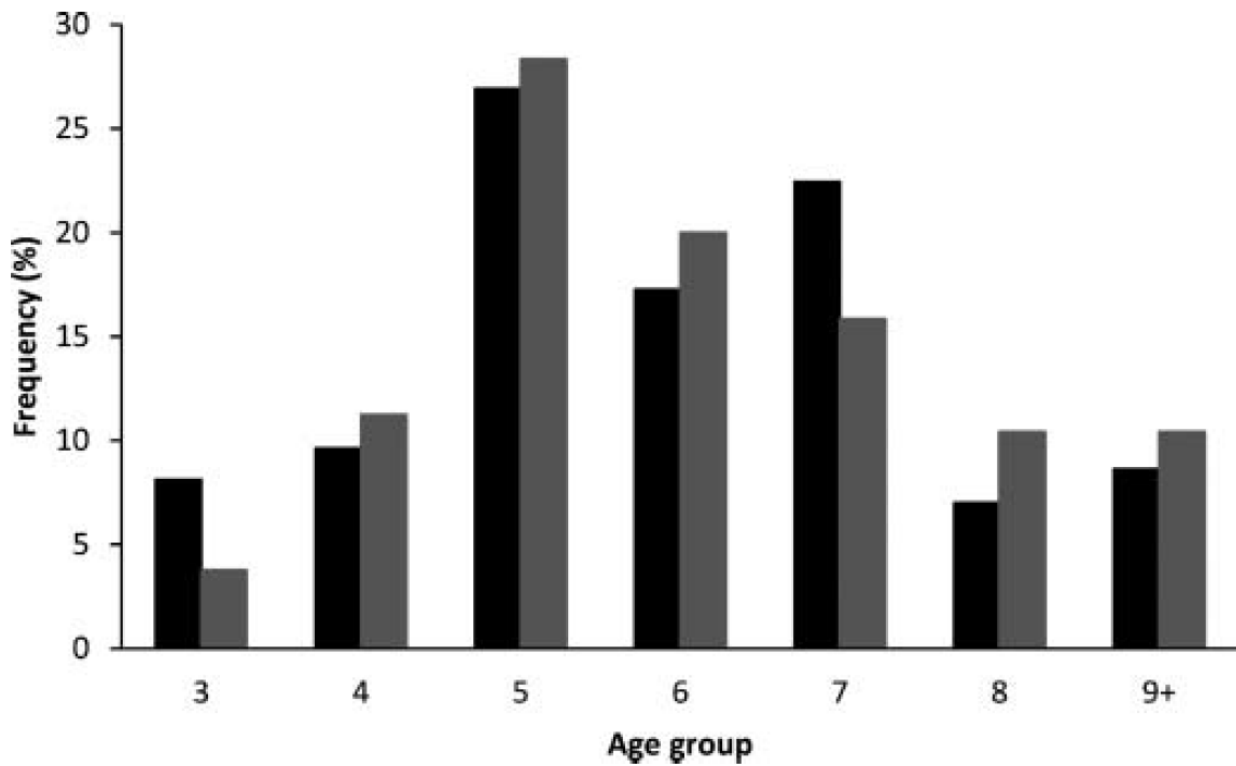


Fig. 17. Comparison of the observed (black bars) and predicted (grey bars) age structure of American eels ascending the Saunders eel ladder in 2006-2008. From Zhu et al. 2013.

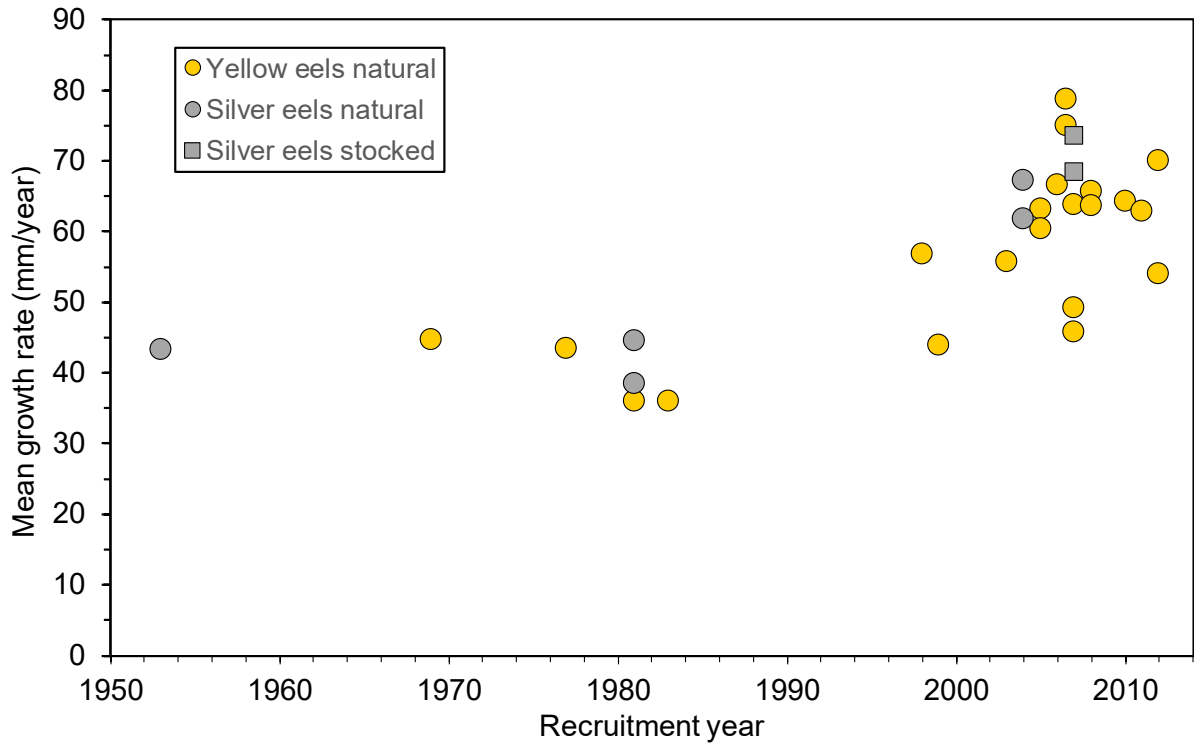


Fig. 18. Mean growth rates of yellow and silver eels in the St. Lawrence Basin between recruitment and the year of sampling, in relation to recruitment year.