

Is the American eel threatened? A Critique of the
COSEWIC 2012 Report

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COSEWIC (2012) Critique

Executive Summary

Introduction

The purpose of this critique is to evaluate the information outlined in the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2012 report and its conclusion that the stock status of the American eel (*Anguilla rostrata*) should be elevated to the “threatened” designation. This most recent report is generally well written and includes many important findings yet we believe that it appears to have either misinterpreted or omitted key data that has led to potentially improper conclusions.

Most recently, the stock status of American eel has been reviewed in several reports by the following:

- (a) Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2006
- (b) U.S. Fish and Wildlife Service (FWS) 2007
- (c) Canadian Science Advisory Secretariat (DFO) 2010
- (d) Atlantic States Marine Fisheries Commission (ASMFC) 2012
- (e) Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2012

With the exception of the COSEWIC (2012) report, all of the above have concluded that the American eel stock status is “of special concern” or “depleted” or not “threatened or endangered” or made no specific assessment. We concur with these former findings and offer the following critique of the “threatened” designation.

Specifically, our concerns include the:

- (a) regional abundance index trends and the over-weighting given to declines in the Lake Ontario-upper St. Lawrence River (LO-USLR) area,
- (b) unjustified weight given to the LO-USLR contribution to the continental population and spawning stock,
- (c) underweighting the potential contribution and importance of unfished, especially estuarine and coastal, areas,
- (d) panmixia and larval dispersal,
- (e) structure of habitat geographic zones and the designatable unit concept in relation to freshwater ecological areas (FEAs) in Canada.

Other related issues considered include the justification for an elver fishery, the stock status of the American eel relative to that of the European and Japanese eel, and a hierarchy of stock recovery actions.

The structure of the Executive Summary follows that of the primary report.

Regional abundance index trends

Within both COSEWIC Status Reports (2006, 2012), unjustified weight appears to have been given to the declining trend of yellow eel recruitment and consequently silver eel production in the LO-USLR area and to the conclusion that it represents an equivalently serious decline in continental stock. The simple counting of negative abundance indices versus neutral or positive indices in the LO-USLR and eastern Canada area involves a type of pseudo-replication, where either the samples may be replicated, but are not independent, or the treatments (experimental units) are not replicated. LO-USLR indices are not independent of each other; they are simply

different measurements of the same regional phenomenon. Furthermore, most of the negative abundance indices in eastern Canada are problematic in that assessment. There is no doubt that the eel stock of the LO-USLR area has declined severely and little doubt that the causes are primarily inadequate fish passage for upstream migrant recruits and historical over-exploitation (COSEWIC 2006, 2012). In eastern Canada most recruitment indices are neutral or positive. Canadian elver and American young-of-the-year (YOY) indices show variability but no evidence of significant decline for more than 20 years. In 2011, 2012, and preliminarily in 2013 elver recruitment indices have reached record highs for many sites. A Generalized Linear Model (GLM)-standardized index of American yellow eel abundance also shows variability but no overall trend over the past 44 years. Since many yellow eel indices occur in areas of active fishing and are substantially based on eels of fishable size, elver indices are a more reliable indicator of continental recruitment. Thus, we conclude that any decline in the LO-USLR area is not representative of the Atlantic coastal situation and is due to local exploitation and inadequate fish passage.

Contribution of the LO-USLR area to the spawning stock

As with the regional abundance indices, unjustified influence appears to have been also given to the LO-USLR area and its contribution to spawning in the COSEWIC Status Reports (2006, 2012). The COSEWIC (2006) report estimates are based on two methods: (1) river discharge attraction and (2) commercial landings. The river discharge method assumes egg production proportional to river discharge; the commercial landings method assumes egg production proportional to regional landings.

With the river discharge method, the percentage of estimated continental egg production from the LO-USLR area ranged from 60.3% to 67.2% depending on whether the Mississippi River basin was included or excluded. The total Canadian contribution was estimated as 93.1% or 83.6%, respectively. Particularly problematic is the assumption of a linear relation between discharge and recruitment. The commercial landings method estimated an LO-USLR contribution of 26.4%. Both methods have substantial biases and undoubtedly overestimate the contribution to total American eel egg production by the LO-USLR area. Neither method considers the potential production of the unfished estuarine/coastal areas of the Gulf of St. Lawrence, an important oversight. Eel fishing occurs in about 6.4% of estuarine and coastal eel habitat areas in the Gulf of St. Lawrence, which includes the St. Lawrence River Estuary, Atlantic-Fundy, and Newfoundland areas.

The COSEWIC 2012 report states that the LO-USLR area is a significant portion of the distribution. Significant is quantified as 5.9% of the occupied biological area or 19% of the area of occurrence (COSEWIC 2012, Table 2), with the former measure being the most relevant.

An alternative approach hypothesises that terrestrial food quantity and quality is primarily responsible for the geographical patterns observed in animal size, abundance and biomass (Huston and Wolverton 2011). This concept specifically addresses the ecologically and evolutionarily relevant net primary productivity (eNPP in $\text{g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$) available for animal feeding and growth during the growing season. Latitudinal gradients in productivity occur both oceanically and continentally, within which coastal saltwater to freshwater gradients occur. Assuming freshwater and estuarine/coastal

productivity and biomass is linearly related to regional terrestrial productivity, American eel productivity/biomass should be related to the maximum eNPP in the latitudes 35-45 °N. This is consistent with generally agreed maximum eel production in the U.S. mid-Atlantic states and LO-USLR area due to the southwestern origin of Lake Ontario and the St. Lawrence River relative to its mouth. The method estimates a relative egg production of 15.7% for the LO-USLR area and 58.1% for Canada, each substantially lower than estimates provided by the COSEWIC (2006) report. This implies that the LO-USLR area may be an important but not critical area to American eel production, as concluded by the FWS (2007) and ASMFC (2012) reports.

Importance of unfished areas

The COSEWIC (2006, 2012), FWS (2007) and ASMFC (2012) reports unduly focus on the decline of exploited river stocks yet underemphasize the potential contribution of unfished areas. While U.S. reports recognize the importance of estuarine and coastal production areas because large fisheries occur locally in such regions as the Delaware and Chesapeake Bays, the COSEWIC (2006) report gives little weight to this issue due to an absence of relevant data at that time. More recent analysis indicates an estimated 9,648 km² of sheltered waters occur along the Atlantic coast and Gulf of St. Lawrence Estuary with eel fisheries found in only about 6.4% of this area. In the estuary and Gulf of St. Lawrence about 2,066 km² of the sheltered waters were classified as intertidal habitat. About 94% of regional eel fishing activity occurs within sheltered habitat.

In the U.S., estimates of nearshore habitat (the zone that includes tidal freshwater and the estuarine mixing area to the seawater edge) total 68,453 km² for four (4) zones from the North Atlantic to the Gulf of Mexico (ASMFC 2000, FWS 2007). The area occupied by fisheries is unknown but a substantial portion is undoubtedly unfished. An estimated 84% of available U.S. freshwater riverine habitat (556,801 km) has been obstructed to some degree by dams, with the degree increasing proportional to dam height (FWS 2007). Estimates of available freshwater and estuarine habitat for American eels in Canada and the U.S. indicate that total Canadian eel habitat comprises approximately 35% of continental habitat. The LO-USLR area contributes about 12% of total Canadian rearing area or 4% of total continental rearing region. The implication is that eel production from the LO-USLR area, while important, is not critical to the Canadian contribution of eel spawners. Nor is it critical to the total North American contribution despite the high female composition, large size and high individual fecundity of eels from the LO-USLR area.

Panmixia and larval dispersal

Recent evidence based on neutral genetic markers supports panmixia in the American eel and the European eel. Panmixia has never been rejected by studies using such markers because genetic differentiation is tested against the null hypothesis of panmixia. Failure to reject the hypothesis is the frequent result. No specific test of the panmixia hypothesis has yet been made for the American eel but methods have been proposed.

Recent evidence indicates quantitative genetic differences in growth rate of American glass eels from two Canadian sites (Atlantic coast, St. Lawrence River). Differences in silver eel growth rates also occur between American eels from Atlantic coastal areas and from the Gulf of St. Lawrence and St. Lawrence River. Differences also occur in neutral genetic markers over the Atlantic coastal range between Florida and the St. Lawrence River due to patterns of spatially (geographically) varying selection. Such differences could arise for several reasons:

- (a) non-random dispersal of spawners or larvae,
- (b) selective mortality based on individual genetic differences,
- (c) passive genotype-specific habitat distribution if the genes associated with environmental variables control leptocephalus stage duration. This possibility conflicts with other evidence.

However, non-random dispersal and individual genetic differences may conflict with the random dispersal assumption often associated with the panmixia paradigm (COSEWIC 2006, ASMFC 2012), which lacks direct evidence to support it. Evidence against random dispersal includes:

- (a) geographic variation in the abundance of larval and glass eels/elvers, including hybrid distribution,
- (b) lack of agreement with observed timing and relative abundance of elver recruitment by latitude,
- (c) absence of a mechanism to explain the timing of larval metamorphosis,
- (d) the uncertain benefit of large size, high fecundity, and high abundance of female American eels to recruitment to a region such as the LO-USLR area

under random distribution rather than as compensation for high mortality enroute to distant regions. The species as a whole may benefit from such production if survival is similar at all latitudes, an uncertain proposition.

Phenotypic response to regional environmental conditions is the presumed explanation for the observed regional differences in American eel life history traits such as age and size at maturity. However, no comprehensive explanation exists for how such environmental conditions control the expression of such traits. The temperature-size rule (TSR) is one hypothesis to explain the observed high phenotypic plasticity in growth and age-at-maturity associated with geographic (latitudinal) variation in seasonal water temperatures and growth period yet offers no single comprehensive explanation. Proximate mechanisms may operate in different species or at varying rates. The ability to react phenotypically must have an underlying genetic mechanism(s) but the mode of operation is uncertain. A genetic link may exist between the increasing elver size and age at recruitment. It may also exist if female spawner size at maturation with increasing northern latitude and larval metamorphosis is controlled by a biological clock. Such a mechanism implies that a decline in spawner escapement from a given area primarily affects recruitment to that area rather than having a wider impact on the continental stock. Consequently, improvements to the spawning escapement from the LO-USLR area would depend largely on regional improvements to fish passage and reduction of turbine mortality at hydroelectric dams and fishing exploitation and not on fishery management actions outside of this region. Mitigation measures taken since the mid-1990s have reduced fishery exploitation, improved fish passage at some dams and developed elver stocking programs for Lake Ontario and two Quebec sites. However,

stocking has recently been curtailed by the potential for transmission of the *Anguillicoloides crassus* parasite.

Further research into anguillid eel genetics and larval metamorphosis and distribution under the panmixia paradigm is required for a better understanding of this complicated issue.

The structure of habitat geographic zones (designatable units)

The COSEWIC (2006) report notes that “sub-speciation, geographic heterogeneity, range disjunction, or biogeographic distinction have not been demonstrated in the American eel population”, thus no consideration was given to assessment below the species level. Recent studies suggest that American eel in the Gulf of St. Lawrence and St. Lawrence River drainage area may have genetically unique growth rate characteristics that merit special protection even within the panmixia concept. Coupled with an exceptionally low juvenile recruitment to the LO-USLR area and relatively more stable glass eel/elver recruitment to Atlantic coastal areas of Canada and the U.S., a more appropriate status assessment would distinguish between the Gulf of St. Lawrence and St. Lawrence River drainage area and the remaining Canadian freshwater ecological areas (FEAs), as defined by COSEWIC (2006).

Justification for an elver fishery

An elver fishery is most justified where elver finite mortality rates are high (>99%), as they may be in many Atlantic coastal and Bay of Fundy streams, presumably due to high predation by resident eels and other predatory fishes and other environmental factors. Density-dependent mortality would be expected to rise with increasing recruitment level. Annual exploitation rates by a fishery of 30-50% of the elver run may have little effect on the abundance of yellow and silver eel production when the elver mortality rate is high.

Since inception, the elver fishery has been tightly controlled by limiting the number of licenses to nine, restricting each licensee to a defined geographic area, and authorizing licensees to fish only specific rivers within that area. Additional controls include:

- (a) the prevention of elver fisheries in rivers with an existing fishery for larger eels,
- (b) restrictions on the type and quantity of fishing gear used, other than dip-nets,
- (c) requiring the live release of other species,
- (c) an overall quota of 1000 kg per license (later reduced to 900 kg) with a limit of 300 kg from any river,
- (d) a requirement that licensees submit daily records of catch and fishing effort by gear type.

The value of the elver fishery has exceeded that for the traditional yellow and silver eel fisheries since about 1995 (Jessop 1995, 2000a), particularly at recent record high elver prices. Elver prices have historically fluctuated greatly. Consequently, the

elver fishery may provide substantial economic benefits to rural regions often characterized by limited and seasonal employment opportunities.

American eel status relative to European and Japanese eel

Historically, American eels have not been as heavily fished as European and Japanese eel, except perhaps in certain areas such as the LO-USLR and mid-Atlantic states/Chesapeake Bay. European and Japanese fisheries may allow fishing of all life stages (elver, yellow, silver eel) in a river system compared to only one or at most two stages in any U.S. or Canadian river system. The stable Canadian elver indices since 1996, American elver indices since 2000 and the large habitat areas that are unfished suggest that American eel recruitment may not be affected to the same extent by the factors affecting European eel recruitment. Oceanic factors may affect larval recruitment to both North America and Europe but the migration path for American eel is less than half that for European eel and thus oceanic factors may have a proportionately lesser effect. The implication is that a well managed elver fishery is not detrimental to either regional or continental eel abundance.

Stock recovery actions

Commercial fisheries tend to be disproportionately targeted due to their ease of control but it is essential that other management options also be utilized. Recent changes in fishery management regulations in Canada and the U.S. include reducing the number of licenses, increasing minimum size limits, restricting fishing seasons, etc. These controls have not been matched by provisions to improve fish passage, both

upstream and downstream, at more than a few of the many hydroelectric dams obstructing potential eel habitat. The difficulty (cost, feasibility, implementation time, etc.) of increasing habitat availability in the LO-USLR area by improving fish passage at dams, particularly hydroelectric dams, is substantial.

Implementation of measures to improve fish passage at man-made obstructions may take 40 years or more and will only be achieved if strong action by provincial and federal regulatory agencies is taken. Such actions would allow for improvements in stock abundance many times greater than further controls on the fishery or even its elimination. We believe that the latter actions would be unjustified, particularly given our contention that the continental stock is not endangered but is stable at a level lower than historic highs.

The management goal of restoring the stock to the landings value levels of the mid-1980s (DFO 2010, COSEWIC 2012) may be unrealistic. A more sustainable goal is required.

Summary

In summary, we believe available evidence provides no justification for the COSEWIC (2012) report to increase the American eel threat level status from “of special concern” to “threatened” and urge that the status level be revised to its previous level.

Critique for the Canadian Committee for a Sustainable Eel Fishery of the
COSEWIC 2012 Report

Introduction

The stock status of the American eel (*Anguilla rostrata*) has most recently been reviewed in reports by (1) the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (2006 and 2012); (2) the U.S. Department of the Interior, Fish and Wildlife Service, 50 CFR Part 17 report on Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition to List the American Eel as Threatened or Endangered, Federal Register Vol. 72, No. 22, pp. 4967-4997 (2007); (3) the Department of Fisheries and Oceans, Canadian Science Advisory Secretariat (CSAS) 2010 Science Advisory Report (DFO 2010); and (4) the Atlantic States Marine Fisheries Commission (ASMFC) American Eel Benchmark Stock Assessment (2012), which includes the associated Terms of Reference & Advisory Report of the American Eel Stock Assessment Peer Review and the American Eel Stock Assessment for Peer Review.

The COSEWIC (2006) report assesses the American eel stock status as “special concern” but the FWS (2007) report could not find evidence to support listing the American eel as either threatened or endangered. The DFO (2010) report makes no continental stock assessment but notes the occurrence of regional variations in abundance indicators, and the ASMFC (2012) report found only that the stock abundance was “depleted” with no definition of depleted offered. We concur with these

findings, which provide no justification for increasing the stock status level to “threatened” as done by the COSEWIC (2012) report. These reports provide a thorough analysis of the data on American eel biology and stock status available at the time of review and publication, that in conjunction with recent data on elver indices and new interpretations of available data, provide the basis for the following critique of the COSEWIC decision to increase the American eel threat level assessment from “special concern” in the COSEWIC (2006) report to “threatened” in the COSEWIC (2012) report. These concerns include: (a) unjustified weight given to declining index trends in the Lake Ontario-Upper St. Lawrence River (LO-USLR) area; (b) unjustified weight given to the LO-USLR contribution to the continental population and spawning stock; (c) underweighting of the potential contribution of unfished areas; (d) panmixia and its complications; (e) the justification for an elver fishery; (f) the stock status of the American eel relative to that of the European and Japanese eel, (g) the desirability of revision to the designatable unit concept in relation to freshwater ecological areas (FEAs) in Canada; and (h) a hierarchy of stock recovery actions.

COSEWIC (2012) Status Assessment Criteria

The 2012 COSEWIC designation of the American eel stock status as threatened was based on assessment criteria A2b. That is, *“an observed, estimated, inferred or suspected reduction of $\geq 30\%$ in the total number of mature individuals over the last 10 years or 3 generations, whichever is the longer, where the reduction or its causes may not have ceased or may not be understood or may not be reversible, based on (b) an index of abundance appropriate to the taxon”*. The indices of abundance used include

fishery-independent indicators and fishery-dependent commercial landings. Although the geographic distribution of the American eel ranges over 50 degrees of latitude from northern South America, through the Caribbean Sea, to south-western Greenland, the population management unit for Canadian purposes is the portion that resides in Canadian waters (COSEWIC 2006, 2012). The Canadian eel habitat has been divided into five (5) ecozones, or freshwater ecological areas (FEAs), to accommodate the observed geographic distributions in American eel size, age, and sex ratio, types and magnitudes of threats, and potential contributions to the spawning stock (COSEWIC 2006, 2012). Coordinated international management of the American eel stock has often been advocated, most recently in the ASMFC (2012) report.

Since the COSEWIC (2006) Status Report, substantial actions by the Ontario, Quebec and Atlantic provinces have been made with the objective of reducing eel mortality from all sources by 50% relative to the 1997-2002 average (DFO 2010, COSEWIC 2012). A draft national American eel management plan has not yet been officially adopted but regional management actions consistent with the plan have been enacted. In response to the drastic decline of American eel abundance in Lake Ontario, the species has been identified as “endangered” under Ontario’s Endangered Species Act and the eel fishery closed. The severity of this decline has no parallel in any other river or lake with unimpeded fish passage.

Acceptance by the Ministers of the Environment and Department of Fisheries and Oceans of a “threatened” designation for the American eel would require more drastic action under the Species at Risk Act (SARA) such as closure of all fisheries and prohibition of sale. We believe such action would be unjustified. Any application to

have the American eel listed under the Convention for International Trade in Endangered Species of Wild Fauna and Flora (CITES), Part II, may also be negated by a reassessment and reduction of the SARA threat level from “threatened” to “special concern”.

This critique examines various interpretations of the available scientific information that we believe are flawed by misinterpretation, unwarranted emphasis, or unjustified hypothesis. Inevitably, these criticisms are extensively interlinked.

Regional abundance index trends

Unjustified weight may have been given to the declining trend of yellow eel recruitment, abundance, and consequent silver eel production in the LO-USLR area by the COSEWIC (2006, 2012) Status Reports and the effects on the continental stock of that decline. Completion of the Beauharnois Dam in the early 1940s and associated Beauharnois Canal on the St. Lawrence River at the upstream end of Lake St. Louis plus several smaller dams on the river’s main channel provided the furthest downstream, and first-encountered, man-made obstructions to upstream passage by American eels (Verdon and Desrochers 2003). Eels were able to maintain passage via the St. Lawrence Seaway. Between 1954 and 1959, construction of the Moses-Saunders Dam further upstream further reduced fish passage; fish passage was provided in 1974, with no passage between 1958 and 1974 (McGrath et al. 2003) other than by nearby ship navigation locks. Reduced recruitment to Moses-Saunders Dam began after 1983. Fish ladder efficiency was estimated at 47-79% and another fishway was added to the Moses-Saunders Dam in 2006. Anthropogenic mortality is estimated

at about 53% of the silver eel run, of which about 75% is caused by turbine mortality (Verrault and Dumont 2003). The Lake St. Francis eel fishery increased substantially after 1986 and, in conjunction with decreased ship-lock use at Beauharnois Dam, was associated with the decrease in eels caught at the Moses-Saunders dam (Verdon and Desrochers 2003). The density-movement hypothesis (Feunteun et al. 2003), whereby eel movement upstream is encouraged by higher densities downstream, may help to explain the effect of the Lake St. Francis fishery, which depleted the resident yellow eel stock, on the movement of juvenile eels to Beauharnois Dam and ultimately to the Moses-Saunders Dam.

The overall mean age of Canadian silver eels is estimated at about 19.3 years (18.6 years, COSEWIC 2012), producing a generation time of about 22 years after consideration for the time of migration to and from the spawning area (COSEWIC 2006). Completion of the Moses-Saunders Dam in 1959 and no fish passage provision until 1974 arguably led directly to the declines in the Lake Ontario trawl fishery (after 1982) and electrofishing (after 1989) indices during the 1980s, a time difference of about one generation. The declining abundance in Lake Ontario after the 1980s contributed substantially to the declining catch of silver eels in the upper St. Lawrence River (Quebec) eel fishery after the mid-1980s (COSEWIC 2006, 2012). The Moses-Saunders Dam eel index declined greatly after 1982 and has only recently (mid-2000s) begun to show small signs of recovery. Restrictions to and reductions in the yellow and silver eel fisheries of the USLR during the mid-2000s may have contributed to this recovery (DFO 2010). Generally, the construction of hydroelectric dams in, primarily, the upper St. Lawrence River watershed has been estimated to reduce potential silver

eel production by over 800,000 eels (Verreault et al. 2004), a figure approximating the number of silver eels caught during the commercial catch peak of the 1920s and 1930s (Fig. 11, COSEWIC 2006). MacGregor et al. (2010) provide a comprehensive examination of eel habitat lost by the construction of dams in the Lake Ontario and upper St. Lawrence River regions.

The eel recruitment decline to the Richelieu R. had a similar timing (after 1981) to that for the LO-USLR and was partly caused by fish passage problems at downstream dams (Verdon et al. 2003). However, the similar timing of declines in both areas has been accepted as evidence of a widespread reduction in eel recruitment to the upper St. Lawrence River area and beyond (COSEWIC 2006). The decline in LO-USLR eel harvest and abundance began in the 1990s.

There is no doubt that the eel stock of the LO-USLR area has declined severely and little doubt that the causes are primarily inadequate fish passage and over-exploitation coupled with low regional recruitment. The CSAS 2010 Science Advisory Report (DFO 2010) states that: "Few abundance indicators of the American Eel in Canada extend from the 1980s to the present. All three Ontario abundance indices are presently at about 3% of the levels measured in the mid-1980s. Counts at the eel ladders at the Beauharnois Dam upstream of Montreal, as well as at the MSGS (Moses-Saunders Generating Station), indicate a recent increase in eel recruitment into LO-USLR since 2003, but are still about two orders of magnitude below the 1980s level." The counts at the Moses-Saunders Dam have continued their increase (Verreault et al. 2012). Much of the decline in production of eels from the LO-USLR can be attributed to inadequate fish passage at dams prior to the 1980s, the development of the Lake St.

Francis yellow eel fishery, and hydroelectric dam turbine mortality on downstream silver eel movement (Verreault and Dumont 2003, Verreault et al. 2004, COSEWIC 2012).

Historic catch levels in LO-USLR are negatively correlated with landings reported 13-20 years earlier, with the highest correlation at 16 years lag, a time difference of about one generation (Robitaille et al. 2003). This shows the effect of fishing effort on regional stock size, although the effect of recruitment is also important. The Lake Ontario eel catch is closely related to the passage of eels at the Moses-Saunders Dam with a lag of about 8 years (Mathers and Stewart 2009).

The meaning and importance to the continental spawning stock of this abundance decline in the LO-USLR is a critical question. The COSEWIC (2012) report does not evaluate this issue other than by declaring that the LO-USLR area represents 19% of the freshwater runoff in the species range and stating that the Table 2 data on the extent of occurrence (19%) and area of occupancy (5.9%) by freshwater biogeographic zone (km²) is significant. The case for declaring the American eel status as threatened seems largely based on the degree of decline in abundance indices (>30% over three generations) in the LO-USLR area (criterion A2b).

Indices of abundance in Canadian areas outside the LO-USLR area show mixed trends. Region-specific status indicators are at similar levels to those reported in COSEWIC (2006), with very low abundance for LO-USLR and variable trends, including declines, no change, or increases, in the Atlantic provinces (DFO 2010, COSEWIC 2012). The COSEWIC (2012) report examines these trends in greater detail but appears to emphasize the negative (e.g. p.iii, lines 2-3), and this pattern continues in the discussion of non-LO-USLR indices. The COSEWIC (2012) report is unclear on the

matter but presumably gives greater weight to the statistically significant than to non-significant increases or decreases. The 11 available abundance indices for the Gulf of St. Lawrence and Atlantic Region (p. 47-56) can be grouped as follows: (a) four significant declines, of which two have undiscussed potential problems (e.g., LaHave River electrofishing index (Fig. 18B)), (b) six with no significant trend, (two elver fishery indices (Fig. 16), one NB yellow eel index (Miramichi River, Fig. 17A), two NB electrofishing indices (Fig. 18A), Western Arm Brook yellow eel count (Fig. 22B)), and (c) one significant increase (Restigouche River yellow eel index, Fig. 17B).

Of the questionable significant declines, the decrease in the electrofishing index on the LaHave River after 2000 fails to consider the potential negative effects on eel passage of the 1996 development of a hydro-electric plant at Morgan Falls, where the decline begins about four years after plant opening, a sufficient period for elvers to attain electrofishing catchability. The two Newfoundland electrofishing surveys have time series at least 13 years out of date. The all NFBZ catch trend (Fig. 24) decline is primarily influenced by the Lake Ontario-Upper St. Lawrence River (LO-USLR) declines.

Three other reported catch reviews have no statistical analysis other than plots and a comparison of period means: Gulf Region reported landings show an increase (Fig. 19 and text last paragraph p. 51), Scotia-Fundy (now Maritime) Region reported landings show a decrease (Fig. 19 and text first paragraph p. 53), and Newfoundland/Labrador reported decreased landings in recent years but an increase over the 1961-2009 time period (Fig. 23). The fishery catch decline in Scotia-Fundy (now Maritime) Region after about 2004 does not consider the effects of the DFO fishery catch reduction policy implemented in 2005 or the possibility of incomplete

reporting (p. 53) while the Newfoundland-Labrador commercial catch trends in recent years (and plausibly in previous years) may have been influenced by market conditions.

The interpretation of Table 6 (p. 59), which is essentially a text version of the associated index plots in the COSEWIC (2012) report, is problematic. The statement “Out of the eight Canadian series allowing percent change evaluation from the 1950s through to the 2000s, seven show negative values (from -17.5% to -96.2%), including data from all areas (Table 6)” is an example of pseudo-replication. Five of the eight series are from the LO-USLR area and illustrate the same phenomenon, measured by different methods, which is the undisputable decline in eel abundance in that area. Therefore, the series are not independent and should be treated as one for purposes of comparison with other regions.

Two negative indices from Atlantic Canada are also problematic. The Table 6 conclusion that the Miramichi River index has a negative trend overlooks the non-significance of this trend reported in Fig. 17. The Table 6 start of the Landings NFBZ1, 8, 2 index at 1970 rather than at an earlier or later date in their time series conveniently chooses the time series peak following a period of, arguably, fishing-up and over-exploitation which is naturally followed by decline. If a 1974 start had been chosen, little evidence of decline would be found. Consequently, eel stock status outside the LO-USLR area is not as dire as within it.

The above concerns carry over into the p. 60, paragraph 1 statement on the shorter time series (1990s to 2000s) that states, “While the clear majority of indices strongly suggest consistent and steep declines both in juvenile and adult indices of abundance within the Lake Ontario - upper St. Lawrence River area, trends across the

rest of the range are highly variable both temporally and spatially.” Problems with the Atlantic Canada indices in Table 6 include the counting of the non-significant negative trend for the Conne River index as negative, the dependence of the significant negative trend for the Western Arm Brook index on a single value (1998), and the possibility that the -17.5% decline in the landings (NFBZ1,8,2) from the 1990s to 2000s arises substantially from the 22% reduction in fishing mortality in eastern Canada during 2005-2010 as a result of changes in the fishery regulations (p. 58, paragraph 1). If these indices are accepted as neutral, then the Eastern Canada indices of Table 6 show neutral (three cases) to increasing (four cases) population trends while those of the LO-USLR area show six declines, with two minor exceptions.

In the United States, a GLM-standardized index of abundance for yellow eels along the Atlantic coast between 1967 and 2010 (44 years) showed considerable variability but no overall trend (ASMFC 2012, Fig. 6.3). Recent yellow eel index values are near the long-term mean but below the time series peak of the mid-1980s. United States yellow eel index values in the mid-2000s were above the long term mean, unlike the stable low values at the Moses-Saunders Dam since the mid-1990s (Marcogliese and Casselman 2009, Fig. 5). This suggests that the Moses-Saunders Dam index is not representative of the Atlantic coastal situation. Most of the indices outside of the LO-USLR area indicate relatively stable, if not increasing, eel abundance.

Other than the ASMFC YOY indices, the majority of non-ASMFC eel recruitment/abundance indicators are from the Delaware Bay/Mid-Atlantic Coastal Bays and Chesapeake Bay region which creates a spatial bias in the data (ASMFC 2012). Most of these surveys were designed for other species and suffer from very low annual

catches of American eels (ASMFC 2012) and occur in areas heavily fished for yellow eels (Weeder and Hammond 2009). The minimum catch size in many states is 6 inches (152 mm), a size at the lower end of the catch size range of many trawl survey nets (ASMFC 2012). Given the known effects of overfishing on yellow eel abundance, it is unsurprising that the indices are low value but 10 of 18 yellow eel indices show either no or a rising trend (ASMFC 2012, Table 6.16). More recently, Nesslage et al. (2012) have found that most fishery-independent U.S. abundance indices from the Delaware Bay and mid-Atlantic coastal bays, including Chesapeake Bay, which are the major production areas, have increased recently, although declining trends generally continue elsewhere.

It is unknown whether declines in U.S. estuarine yellow eel fisheries and abundance indices produce equivalent declines in silver eel production in unfished inland river areas. There are few silver eel fisheries in the U.S., particularly in the Mid-Atlantic States area, and poor knowledge of potential silver eel production or escapement. Heavy fishing of estuarine areas may reduce the number of eels migrating upstream based on the density-movement hypothesis (Feunteun et al. 2003), thus reducing upstream silver eel production but potentially increasing the proportion of females. However, removal of dams obstructing upstream movement of eels results in greatly increased densities of eels in upriver reaches and may increase eel population growth rates as a result of increased female eel abundance and size/fecundity (Hitt et al. 2012).

The use of historical and recent American eel commercial landings data in a depletion-based stock reduction analysis (DB-SRA) to examine coast-wide stock

biomass trends in U.S. waters resulted in a conclusion that the American eel stock is currently depleted, but with no definition of depleted (ASMFC 2012). Current stock biomass estimates are at levels above the long-term mean values seen historically for long periods prior to recovery. This suggests no significant threat of stock extinction if appropriate management recovery actions occur. The caveats associated with the model are well covered. However, the estimate of habitat eel carrying capacity is based on the area occupied by fisheries and does not account for areas without them. The latter may be a substantial portion of the available continental habitat if the U.S. situation is comparable to Canada because most fisheries harvest yellow eels that have a relatively small home range. This overestimates the degree of current depletion on a continental basis although not necessarily for the local area of fishery activity. Further, it is unclear that any current and future reductions in fishing effort and catch due to management regulation or commercial market changes will result in increasing estimates of available biomass. The opposite would be more likely expected because the model has no method of weighting or accounting for fishing effort. The Review Panel recommended that the influence of later maturation ages should be explored. The double M-stanza model approach could be analogously extended to a double age-at-maturation stanza model to account for the observed latitudinal differences in age at maturation (Jessop 2010).

The current central paradigm of American (indeed anguillid) eel reproduction assumes panmixia, a breeding system in which all members of a species mate randomly as a single breeding population with no geographic genetic heterogeneity (in neutral genetic markers) (COSEWIC 2006, p.6; ASMFC 2012, p.6), and stochastic

(random) larval dispersal in abundance (COSEWIC 2006, p.13; ASMFC 2012, p.6).

The latter hypothesis is distinct from the first and not essential to it yet has a major, wide-ranging effect on the interpretation of available data. The random larval dispersal hypothesis is unsatisfactory in several respects, most importantly, a lack of direct evidence to support it. The COSEWIC (2012) report does not discuss the issue of random larval dispersal.

Under the panmixia hypothesis of American eel reproduction, the decline in recruitment of yellow eels to the USLR hydroelectric dams in Canada and in some U.S. yellow eel indices has been interpreted as a reflection of recruitment decline to the entire Atlantic coast. However, the absence of trend in elver abundance indices in Atlantic coastal Canada and the United States during periods when yellow eel recruitment indices continued to decline or bottomed out must be given equal weight because they indicate recruitment untainted by potential fishing effects. The geographic extent of the elver indices equals that of the yellow eel indices (ASMFC 2012). Region-specific yellow eel indices were not statistically correlated (Spearman's rank correlation, $\alpha < 0.10$) with lagged YOY (young-of-the-year) indices in 23 of 25 comparisons (ASMFC 2012, Table 6.4). The probability of finding one or more statistically significant results in 25 tests is 0.93 and the probability of two tests being significant due to chance alone is 0.27 (Moran 2003). The YOY indices may best reflect continental recruitment while the yellow eel indices arguably reflect the degree of local overfishing and, in the case of the LO-USLR area, the additional effects of inadequate fish passage (COSEWIC 2012).

The East River, Chester, NS elver index has shown substantial annual variability but no trend for the past 16 years (1996-2012), although the index was not conducted

between 2003 and 2007 (Jessop 2003a, DFO 2010). The 2011 and 2012 indices have been among the highest recorded (Fig. 1) and preliminary data indicate that the 2013 index will be comparably high. The East River, Sheet Harbour index conducted between 1990 and 1999 also showed no trend. The correlation between the overlapping four years (1996-1999) was 0.998, $p = 0.004$ and extends the time series to 22 years. The very low sample size biases low the estimates of r and significance value but this is only of concern if r is marginally non-significant.

Commercial fishery elver landings have varied widely over time but 2012 landings were near their historic peak despite a recent reduction in quota (Fig. 2). Elver fishers in the Maritime Region report that elver abundances in 2011, 2012, and preliminarily in 2013, were as high as or higher than previously experienced. This enabled fisher quotas of 900 kg, for most licenses, reduced from 1,000 kg in 2005 (total fishery quota now 7,470 kg), to be caught in some areas in record short time periods (pers. comm., G. Carey, Canadian Committee for a Sustainable Eel Fishery). In most years, most fishers have not caught their quota. This may reflect the assignment of equal quotas to fisheries distributed over areas that receive widely differing recruitments (Jessop 1998a).

Catches in the Maine elver fishery have varied between 1994 and 2012 but show no trend after accounting for the reduction in the number of licenses issued and gear fished after 1998 (pers. comm. G. Wippelhauser, Maine Dept. of Marine Resources). Elver catches in Maine between 1994 and 1998 averaged 5070 kg (range 3,338 – 7,529 kg) with the number of licensed gear units (fyke and dip nets) averaging 4,584 nets (range 3,127 – 5,917 nets; no data 1994-1995). From 1999 to 2011, the catch

averaged 2,168 kg (range 582 – 4,379 kg) taken by an average of 691 nets (range 321 – 1,242 nets). The mean catch per net has increased over time, with 2011 having the highest catch per net. The U.S. YOY eel index program that began in 2000-2001 shows essentially stable trends at all sites, with recent increases in 13 of the 16 indices (ASMFC 2012; Table 6.15, Figs 5.18-5.33). In 2011 and 2012, several states had YOY index increases, with some having index series highs (pers. comm., B. Chase, Massachusetts Division of Marine Fisheries, New Bedford, MA). The lack of trend in elver fishery catches and indices since about 1990 is similar to the stable, low level counts of yellow eels at Moses-Saunders Dam (Marcogliese and Casselman 2009), although elver fishery catches and indices and yellow eel counts have increased in recent years. Just how current elver abundances at index rivers might compare to historic values is unknown but it is likely they have fluctuated widely over long time periods as have European eel elver indices (ICES 2012). The coastal elver abundance indices and elver fishery and the Moses-Saunders yellow eel index may reflect different phenomena.

Although strong correlations occurred between abundance indices from the East River, Chester and East River, Sheet Harbour ($r = 0.998$, 130 km apart; Jessop 2003a) and between Little Egg Inlet and Beaufort Inlet ($r = 0.85$, 570 km apart; ASMFC 2012, p.7), there was little correlation between U.S. YOY indices from different geographic areas, with 14 of 113 comparisons (12.4%) being statistically significant (Table 5.9). Statistically significant ($\alpha < 0.10$) Spearman's rank correlations were found between sites within regions in 4 cases (2 positive, 2 negative), between sites in adjacent regions in 5 cases (4 positive, 1 negative), and between sites in distant regions in 5 cases (all

positive). However, the probability of finding one or more significant tests due to chance alone in this group of tests is 0.999 and the probability of finding exactly 14 significant results in the table by chance alone is 0.081(Moran 2003). Thus, the number of significant results may be overstated and significant correlations between distant sites may be suspect. The quality of site data collected, particularly during the early years of the indexing process, and differences in gear efficiencies (dip net, fyke net, Irish elver trap, Sheldon elver trap) may have affected correlation values between sites. The signs of correlations for sites within regions may reflect regional distribution patterns. Regional YOY indices were significantly correlated in 5 of 15 comparisons (ASMFC 2012, Table 6.2), with the Hudson River playing a role in three comparisons. The remaining two significant comparisons were for the adjacent Chesapeake Bay-South Atlantic regions and the distant Gulf of Maine-South Atlantic regions. Given the number of comparisons, there is a probability of 0.79 that one or more significant comparisons occurred by chance (Moran 2003). A reasonable conclusion might be that while small to medium scale YOY distributional patterns may show some coherence, it is largely lost at larger scales.

The U.S. YOY index data are insufficient to evaluate any regional differences in recruitment abundance because some indices are based on relatively small numbers of eels, perhaps reflecting site location or catchability issues. Substantial differences in regional recruitment abundance have been found along the Atlantic and Bay of Fundy coasts of Nova Scotia and New Brunswick (Jessop 1998a). This indicates that abundance can vary greatly at small geographic scale due to local environmental phenomena such as coastal currents.

The density-distribution hypothesis applied to the upstream movement of elvers and yellow eels might also be applied to the coastal distribution of leptocephali and glass eels. If their production was decreased by reduced escapements of spawners from the LO-USLR or by oceanic conditions affecting overall larval survival and recruitment, the effects would be most severely felt at the distribution extremities, such as the LO-USLR, and Newfoundland and Labrador where relevant recruitment information is unavailable. Inadequate fish passage, overfishing, and other factors such as pollution, have probably contributed strongly to the eel abundance decline in the LO-USLR (COSEWIC 2012) but the effect on the species in general is uncertain. It has been assumed to be important based on the high fecundity of large female silver eels produced in the system (Caron et al. 2003, Tremblay 2009). However, there is no good way of assessing the contribution of an estimated 300,000-400,000 silver eels from the USLR to the spawning population in the absence of silver eel production estimates from the remaining continental area. If the hypothesis of random distribution of larvae/glass eels along the continental coast does not apply then the decline of eel abundance in the LO-USLR might not have proportionate effects on the continental population but rather be limited to the LO-USLR stock.

Contribution of the LO-USLR area to the spawning stock

Unjustified influence may have been given to the LO-USLR area in the COSEWIC (2006, 2012) Status Reports. The COSEWIC (2006) report provides estimates of the contribution of the LO-USLR stock to the population spawning stock based on two methods – river discharge, which assumes egg production proportional to

river discharge, and commercial landings, which assumes egg production proportional to regional landings. The percentage of continental egg production from the LO-USLR area estimated by the discharge method ranged from 60.3% to 67.2% depending upon whether the Mississippi River basin was included or excluded. The total Canadian contribution was estimated as 93.1% or 83.6%, respectively. The assumption of a linear relation between discharge and recruitment is particularly problematic as is the underestimation of the continental habitat area, and thus discharge contribution, by restricting it to Canada and the United States (Castonguay et al. 1994, COSEWIC 2006). This omits the habitat represented by Mexico, Central America, the Caribbean Islands, and northern South America. The COSEWIC (2012) report offers little insight into the relative importance of eel production from the LO-USLR area. It simply declares that the 5.9% area of biological occupancy and the 19% area of occurrence are significant (COSEWIC 2012, Table 2). The assertion that the St. Lawrence River runoff represents approximately 19% of the total freshwater runoff in the species range is incorrect – it represents 19% of Canadian and United States discharge (Castonguay et al. 1994) because it excludes “the small part of the range south of the United States” as defined by Scott and Crossman (1973). This is similar to the range descriptions in Leim and Scott (1966) and Scott and Scott (1988). Despite the reference to Panama, this range excludes Mexico, Central America, and northern South America based on the map in Leim and Scott (1966, p.155). COSEWIC seems uncertain of the geographic range of the American eel, with the COSEWIC (2006) map (Fig. 2) indicating a continental range including southern Mexico to Columbia while the COSEWIC (2012) map (Fig. 2) shows a disjunct range that does not include this region although the text

describes it as from Venezuela to Greenland (p. 13). Both Fishbase (2011) and NatureServe (2012) distribution data and maps support a range description that includes Central America and northern South America to Guyana. The area involved appears to be perhaps 5% of the total geographic habitat range but habitat densities are unknown and periodic reported annual catches of 20-40 tonnes of eels (possibly elvers) in countries such as Mexico and the Dominican Republic suggest that moderate juvenile eel populations may be present (ICES 2001, Table 2.1.1.2; ASMFC 2012, Fig. 4.19).

The alternative landings method produced an estimated contribution of 26.4% by the LO-USLR area to continental production. These estimates suggest an important contribution by the LO-USLR area but not one critical to the survival of the species (COSEWIC 2006, FWS 2007). An important oversight is that neither method considers the potential production of the unfished estuarine/coastal areas of the Gulf of St. Lawrence. Combining estimates of the potential egg production by the large silver eel escapement from the LO-USLR area with that of smaller sized silver eels from the Gulf of St. Lawrence and St. Lawrence River estuary (GSL-SLRE) would increase the potential contribution of the area's total spawning stock but reduce the relative importance of the LO-USLR area and the degree of threat to the continental eel population. Cairns et al. (2012) estimate that eel fishing occurs in about 6.4% of estuarine and coastal habitat areas suitable for eel in the GSL-SLRE, Atlantic-Fundy, and Newfoundland areas.

Another approach is based on the hypothesis by Huston and Wolverton (2011) that terrestrial food quantity and quality (eNPP – ecologically and evolutionarily relevant net primary productivity defined as net primary production during the growing season, in

$\text{g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$) is primarily responsible for the geographical patterns observed in animal size, abundance, and biomass. It specifically addresses the net primary productivity available for animal feeding and growth during the growing season. Latitudinal gradients in productivity occur both oceanically and continentally, within which occurs a coastal saltwater/freshwater gradient (Huston and Wolverton 2011). Assuming that freshwater and estuarine/coastal productivity/biomass is linearly related to regional terrestrial productivity, American eel productivity/biomass should be related to the maximum eNPP in the latitudes 35-45 deg N. This is consistent with generally agreed maximum eel production in the mid-Atlantic states (ASMFC 2012) in the U.S. and LO-USLR in Canada (historically if not presently) due to the southwestern origin of Lake Ontario and the St. Lawrence R. relative to its mouth (Fig. 2). However, coastal zone eel production benefits from the moderating effects of a coastal climate relative to the harsher, more continental LO-USLR climate.

In the peak market demand period of the late 1970s and early 1980s (Robitaille et al. 2003), the maximum recorded catch from U.S. Atlantic coastal waters was about 1,620 mt (tonnes) in 1980 (Fig. 5.1, ASMFC 2012). The maximum recorded catch from the LO-USLR area was approximately 220 mt in 1978 (Fig. 2, Mathers and Stewart 2009). If the regional available biomass of American eels is reflected in the catch rate, then the Atlantic coastal area of the U.S. has about 7.4× the biomass of the LO-USLR area. However, the eNPP model suggests that it is approximately 2.0× greater (Table 2). The difference might be due to higher relative exploitation rates in the U.S. Atlantic coastal area than in the LO-USLR area during the time period or perhaps a weakness in the assumption that the historic trend in spawning stock size parallels that in

commercial landings (ICES 2012, Section 8.5). The majority of U.S. catches come from the mid-Atlantic region, primarily the Chesapeake Bay-Delaware Bay area (ASMFC 2012). Eel harvest in the mid-Atlantic states has been primarily yellow eels while most of the harvest in the LO-USLR has been silver eels (ASMFC 2012, COSEWIC 2006). The fecundity of freshwater resident eels in the U.S. Atlantic coastal area is higher than that for estuarine resident eels because they are typically larger than estuarine residents at silvering and migration (Goodwin and Angermeier 2003). Estuarine productivity is generally regarded as high, often higher than freshwater productivity. It is affected by nutrient and detritus flows from associated rivers, intertidal habitats, and the sea and long retention times. This is consistent with high potential eel production in estuaries, perhaps including the upper St. Lawrence River estuary and lower Gulf of St. Lawrence. Eel growth rates are higher in estuarine areas than in freshwater (Jessop et al. 2008). There is no linear change in eNPP with latitude but primary productivity in association with the temperature-size rule (Jessop 2010) could together help explain observed patterns in biomass and size.

Available habitat and productivity ultimately control abundance and biomass, subsequent to regional recruitment abundances. Relations between eNPP and body size, by geographic area and habitat type, produce estimates of relative egg production of 15.7% for the LO-USLR area and 58.1% for Canada (Table 2). This is substantially lower than the estimates provided by the COSEWIC (2006) report. If the LO-USLR fecundity contribution is overestimated relative to that for other areas as suggested previously, it would further overstate the relative importance of the LO-USLR area to continental production. The implication is that the LO-USLR area may be an important

but not critical area to American eel production - a conclusion made by the FWS (2007) and ASMFC (2012) reports. The combining of potential estuarine/freshwater habitat area and biomass production values indicates that the U.S. may play a greater role in American eel sustainability and the LO-USLR area a lesser role than suggested by COSEWIC (2006). This is not to say that habitat losses or over-exploitation in any area should be ignored but it puts the relative management needs in context.

Importance of unfished areas

The COSEWIC (2006, 2012), FWS (2007), and ASMFC (2012) reports unduly focus on the decline of exploited river stocks while underweighting the potential contribution of unfished areas. Further, the U.S. reports recognize the importance of estuarine/coastal production areas because large fisheries occur in such areas as the Delaware and Chesapeake Bays. The COSEWIC (2006) report notes the issue but gives it little weight due to the absence of relevant data at that time. The ICES (2009) report offers the first comprehensive analysis of the estuarine/coastal habitat use by anguillid eels and clearly identifies both its importance and associated uncertainties. The ICES (2012) report notes that an important deficiency for European Union national stock assessments is the absence of eel production estimates for coastal waters. Cairns et al. (2012) estimates that about 9,648 km² (8,910 km² if only 50% of intertidal zone habitat is considered useable) of sheltered waters occur along the Atlantic coast and Gulf of St. Lawrence and estuary, with eel fisheries in approximately 6.4% of this area. In the estuary and Gulf of St. Lawrence about 2,066 km² of the sheltered waters were classified as intertidal habitat, an area with approximately 94% of regional fishing

activity. The average fishery catch was 30.1 kg/km²/yr for sheltered areas. There is a further 23,292 km² of semi-exposed habitat, within which approximately 6% of fishing locations occurred, most of which (83%) are in the St. Lawrence River estuary.

Sheltered and semi-exposed habitat areas in the estuary and Gulf of St. Lawrence total 32,940 km² (Table 1) or 32,202 km² with intertidal zone adjustment.

The CSAS Science Advisory Report (DFO 2010) concludes that any evaluation of anthropogenic mortality on the eastern Canadian eel stock must consider geographic variability. Eel fisheries are unevenly distributed in eastern Canada. Only 7% of the eastern Canadian coastline is within 1 km of an eel fishing site but this value varies from about 1% in Quebec and the Island of Newfoundland to 35% in the southern Gulf of St. Lawrence. Much of eastern Canada has no eel fishing activities, particularly the northern Gulf of St. Lawrence. No broad-scale evaluations of mortality due to fish passage in eastern Canada have been made but whatever the mortality rate, dams, including hydroelectric, are absent from substantial areas of eastern Canada. The implication is that substantial areas of potential eel habitat are unexploited and have no major source of anthropogenic mortality.

In the U.S., estimates of near-shore habitat (tidal freshwater to estuarine mixing area to seawater) total 68,453 km² for four zones from North Atlantic to Gulf of Mexico (ASMFC 2000, FWS 2007) (Table 1). The area occupied by fisheries is unknown but a substantial portion is undoubtedly unfished. Cairns et al. (2013) estimates that U.S. Atlantic coastal sheltered saline water eel habitat plus the semi-exposed areas of the highly productive Delaware and Chesapeake Bays totals 14,360 km². The freshwater habitat area available for eels in the Atlantic coastal U.S. (classified as non-emergent

habitat) plus riverine tidal habitat based on the U.S. Fish and Wildlife Service National Wetlands Inventory (NWI) totals 14,690 km². This is similar to the potential freshwater habitat estimate of 14,080 km² for American eels in Canada (Table 1). Busch et al. (1998) estimated that about 84% of the available freshwater habitat (556,801 km in linear measure) in the U.S. has been obstructed by dams, with the degree of obstruction increasing with increasing dam height (FWS 2007). This linear measure underestimates area because it does not quantify lacustrine area, rivers typically narrow in width as they progress inland, and obstructions tend to increase inland; it then overestimates area by ignoring the habitat reduction due to natural obstructions. In the Hudson River, barriers reduced upstream eel densities by a factor of ten (Machut et al. 2007). Conversely, dam removal can increase instream eel abundance and size composition over long distances e.g., 150 rkm (Hitt et al. 2012). Consequently, it can be concluded that the majority (>50%) of the potentially available eel habitat in Canada is freshwater while freshwater and saline water habitats are approximately equal for the Atlantic coastal U.S. but after natural and man-made obstructions are considered, the available habitat is mainly saline for both countries.

An alternate estimate of U.S. freshwater eel habitat can be made given the assumption that the proportion of freshwater relative to coastal/estuarine is similar to that for Canada (Table 1). The U.S. near-shore area (68,453 km²) can be considered habitat comparable to the sheltered and semi-exposed Canadian categories for the St. Lawrence River estuary, Gulf of St. Lawrence, and Atlantic coastal areas (32,940 km²). The potential Canadian freshwater production area may be about 30% of total Canadian habitat while U.S. freshwater production area may be approximately 23% of total U.S.

habitat. Total Canadian eel habitat comprises about 35% of continental habitat. The LO-USLR area represents approximately 12% of the total Canadian rearing area and 4% of its continental rearing area. These habitat estimates differ from those of Cairns et al. (2013) because they include Gulf of Mexico freshwater and nearshore saline water estimates, thereby reducing the importance of the LO-USLR area relative to the Cairns et al. (2013) data. The implication, in either case, is that eel production from the LO-USLR area, while important, is not critical to the Canadian contribution to eel spawners or to the total North American contribution, despite the high female composition, large size, and high individual fecundity of eels from that area.

Panmixia and larval dispersal

Recent evidence based on neutral genetic markers supports panmixia in the American eel (Gagnaire et al. 2012, Côté et al. 2012) and European eel (Als et al. 2011). However, panmixia cannot be directly tested because it is the null hypothesis against which genetic differentiation is tested. Such tests can only fail to reject the null hypothesis. Côté et al. (2012) found that the minimal level of genetic differentiation detectable with their microsatellite dataset was very small ($F_{ST} = 0.00034$), where F_{ST} is the proportion of genetic variation occurring among populations. In comparison, they measured an extremely weak global genetic differentiation ($F_{ST} = 0.00009$), which was not significantly different from zero ($p=0.998$). Considering the power recently reached by such population genetic studies, any possible deviation from the panmixia model would remain limited to a range of demographic parameters where F_{ST} remains null (i.e. for very large values of $N_e m$, the product between population effective size and

migration). Therefore, although specific tests of the panmixia hypothesis have been proposed (e.g. Beerli and Palczewski 2010), they will unfortunately not solve the “ $F_{ST} = 0$ problem”.

Population genetic tests for panmixia were done using neutral markers that were not directly or indirectly influenced by selection. Indeed, markers of phenotypic traits under spatially varying selection can exhibit variation patterns even under panmixia. This has been recently demonstrated using selected Single Nucleotide Polymorphisms (SNP) markers from the American eel transcriptome (Gagnaire et al. 2012). More than 13000 SNPs located in coding gene regions were screened to find 13 SNPs showing evidence for spatially varying selection. They conclude that even functional genetic variation is most often randomly distributed in the American eel, and that only a small proportion of the genome undergoes spatially varying selection. On the other hand, Côté et al. (2009) report evidence for regional quantitative genetic differences based on variability in growth rate between glass American eels from two Canadian sites (Atlantic coast, St. Lawrence River). Although an apparent discrepancy exists between quantitative phenotypic differences that are easily detectable and genetic frequency patterns that are only found for a small proportion of the genes, it is known that phenotypic traits can show stronger shifts in their geographic frequency pattern than do the genes underlying the trait, particularly for highly polygenic traits. Therefore, adaptive phenotypic traits, such as growth rate or lipid storage capacity, can be used more conveniently to study adaptive genetic variation in eels because genetic spatial frequency patterns are weak when gene flow is high, as in panmixia.

Even under panmixia, individuals are not genetically equivalent if the number of genes associated with ecologically important phenotypic traits is not too large. The situation for eels is unknown. In such circumstances, regional fitness differences may develop with essentially random breeding each generation. Based on the analysis of selected genetic markers, Gagnaire et al. (2012) found evidence that spatially varying selection (i.e. selective mortality based on individual genetic differences) can shape allele frequencies within a single generation over the Atlantic coastal range between Florida and the St. Lawrence River.

Such differences could alternatively arise by non-random dispersal of larvae. For instance, Gagnaire et al. (2012) note that passive genotype-specific habitat “choice” might occur if the genes associated with environmental variables control leptocephalus stage duration. However, they dismiss this possibility because the observation that the early metamorphosing larvae naturally recruit to near the center of the continental distribution range and the later metamorphosing larvae recruit to more northern and southern locations (Wang and Tzeng 1998) is inconsistent with the clinal multilocus spatial component detected at the loci examined. Moreover, these loci showed deviations to Hardy-Weinberg Equilibrium (HWE) in continental but not larval samples. This is incompatible with the habitat “choice” hypothesis but is a strong prediction under the spatially varying selection hypothesis. “Choice” seems a poor word to use in this context but it is a term used in population genetics that does not necessarily imply “active habitat choice”. There is no evidence that larvae actively choose their timing and location of metamorphosis and there is little understanding of how larval metamorphosis is controlled. Habitat choice for glass eels/elvers is largely between

estuarine and freshwater habitat and is a different, but perhaps related, issue based on condition at continental arrival (Edeline et al. 2005, Edeline et al. 2009). Inter-habitat movements by elvers and yellow eels are not uncommon (Jessop et al. 2002). However, selective mortality of relatively unfit larvae/glass eels could occur if geographic regions receive a mix of genotypes that is weighted towards the regional optimum via the timing of leptocephalus metamorphosis and if timing is controlled by a regionally-influenced, genetically-based mechanism. Jessop (2010) proposed a metamorphosis/migration hypothesis that utilizes these concepts.

Non-genetic observations of glass and silver eel growth rates are supportive of hypotheses of quantitative genetic difference (Q_{ST} the proportion of quantitative genetic variation occurring among populations) between American eels from Atlantic coastal areas and the Gulf of St. Lawrence and St. Lawrence River. Quantitative genetic differences in growth rate have been found in a variety of fish species (Conover et al. 2006). Growth rate is a moderately heritable, polygenic trait influenced by pre- and postnatal maternal effects (Falconer 1989). Jessop (2010) found that silver eel growth rate decreased with increasing latitude to about 44 °N, approximately the latitude of the Cabot Strait entrance to the Gulf of St. Lawrence and increased slightly with latitude within the Gulf of St. Lawrence and St. Lawrence River. After adjustment for seasonal water temperatures and length of the growth period, silver eel growth rates were relatively constant along the Atlantic coast up to 44 °N and increased with latitude within the Gulf of St. Lawrence and St. Lawrence River. Côté et al. (2009) and Bernatchez et al. (2011) reported higher growth rates for glass eels from the Atlantic coast site of the Mira River, Cape Breton, N.S. than from the Grande-Rivière-Blanche that drains into the

St. Lawrence River estuary. The conclusion of differences in growth rates between glass eels of different origin can be criticized on the basis that too few eels (10 per tank per time period) were measured to adequately account for the large differential growth rates typical of eels reared in tanks and the resultant occurrence of extremes in eel length (L_T) frequency distributions. Acceptance of this criticism reduces the strength of the conclusion of differential eel growth between regions and of any genetic difference. However, Vladykov and Liew (1982) transplanted elvers from southwestern New Brunswick to ponds in Ontario and found that their growth rates and abundance of males were more typical of their origin than of the receiving waters. More recently, transplanted elvers from the Atlantic coast of Nova Scotia to locations in the lower St. Lawrence River, Lake Champlain, the upper St. Lawrence River, and Lake Ontario also showed characteristics different from those of eels naturally recruited to the receiving waters, including faster growth rate, smaller size at sexual maturation and migration, and a higher proportion of males (Verreault et al. 2009, 2010, Pratt and Threader 2011). Such changes might also be attributed to the holding conditions of the glass eels prior to stocking, to relatively high stocking densities, or both (Pratt and Threader 2011). Higher glass eel growth rates in a laboratory study and in transplantation for Atlantic coastal sites relative to sites in the Gulf of St. Lawrence and further upstream are not necessarily incompatible with higher seasonally-adjusted growth rates for endemic silver eels from within the Gulf of St. Lawrence and upstream.

Evidence is accumulating that locally adaptive mutations may occur and become fixed in the genome even under panmixia (Gagnaire et al. 2012). This contributes to phenotypic plasticity which may be the primary mechanism for adapting to habitat

heterogeneity (Edeline 2007). Phenotypic plasticity describes the ability of individual genotypes to produce different phenotypes (organisms with different characteristics such as growth rate, size at maturation, sex ratio, etc.) Environmentally induced differences in the endocrine system are an important cause of phenotypic plasticity (Dufty et al. 2002). Maternal and other environmental factors can also influence the development of young organisms and can affect the range of physiological and behavioural responses available to them as adults.

Little is known about the migratory process that delivers larval/glass eel stage American eels from the spawning area in the Sargasso Sea to the eastern coast of North America via the Antilles, Florida, and Gulf Stream currents (Tesch 1977, Kleckner and McCleave 1985, McCleave and Kleckner 1987, ASMFC 2012, Righton et al. 2012). Larvae may be distributed southward and into the Caribbean Sea and Gulf of Mexico via the Windward and Mona Passages. The distribution of larvae northward from Cape Hatteras is greater than that southward due to prevailing oceanic currents (Kleckner and McCleave 1985, 1988, McCleave 1993). As the latitude increases, so too do the lengths of American eel leptocephali and most metamorphose to the glass eel stage between about 50-65 mm (Kleckner and McCleave 1985). Metamorphosis results in a reduction in length and weight, with length shrinking by 10-15% for the European eel (Lecomte-Finiger 1994) and perhaps an equivalent amount for the American eel. The mean length (size) of glass eels/elvers increases northward along the Atlantic coast with increasing distance from the spawning area and from the first arrival site near the continental shelf between northern Florida and North Carolina (Jessop 2010, Laflamme et al. 2012) from about 50 mm to 63 mm, as does their age at metamorphosis and

continental arrival (Wang and Tzeng 1998). A similar pattern presumably also occurs southward into the Caribbean Sea and towards Central America. Early maturing larvae begin metamorphosis to the glass eel stage and move shoreward at a younger age and larger size than do those maturing later. This suggests faster growing larvae lead the distributional front. Elver lengths, weight, and condition tend to decline over annual runs, at least north of about Cape Hatteras (Jessop 1998b, Jessop 2003a, Powles and Warlen 2002, Sullivan et al. 2006). Orientation and direct swimming are probably important in enabling leptocephali to detrain from the Gulf Stream and move shoreward but how this is achieved is unknown (Righton et al. 2012). Estimates of American eel larval abundance increased 9-fold between the northern Straits of Florida and Cape Hatteras but relative larval abundances further northward are unavailable (Kleckner and McCleave 1985). Glass eels occur over the continental shelf but, again, no estimates of relative latitudinal abundance are available.

Just what triggers the metamorphosis from leptocephalus larva to glass eel is uncertain (Otake 2003, Miller 2009). The timing of metamorphosis may be a random encounter with the continental shelf as the larvae are carried northward in the Gulf Stream (Kleckner and McCleave 1985, Avise et al. 1986, COSEWIC 2006, p.13). This hypothesis has no supportive evidence. European and American eel hybrids occur, almost exclusively, in Iceland, which suggests hybridization in a specific area of the Sargasso Sea spawning area and subsequent non-random larval dispersal (Als et al. 2011). However, Als et al. (2011) conclude that non-random advection of hybrid eel larvae from a specific area in the Sargasso Sea is unlikely. Although the duration of their larval phase may be intermediate to that of the parental species, there is no

explanation for how such duration might be governed or what triggers metamorphosis. Greater migratory distances have been suggested to offer greater opportunities for intermixing of any putative regional groups. However, if putative regional groups have equal regional adaptability under panmixia, the degree of intermixing is unimportant. If they do not, and differential regional adaptability exists, the degree of intermixing remains unimportant because there must be a mechanism to ensure appropriate regional distribution by regionally adapted groups that would act independent of the degree of intermixing. Rather it is the timing of metamorphosis that takes larvae out of the intermixed group as it moves away from where the earliest arrivals reach the continental coast that is important. Such a process, which progressively reduces the degree of intermixing, may be fundamental to delivering glass eels/elvers to any region. The return of glass eels/elvers to a region of putative parental origin may depend on the appropriate timing of larval metamorphosis.

The timing and duration of larval eel migration is uncertain. Wang and Tzeng (1998 (Table 3), 2000) concluded that the total length of elvers grew with age and both increased with increasing latitude. The post-metamorphic migration period increased with growing elver length, which did not change with older age at metamorphosis. The total age at continental recruitment of American eel elvers increased at higher latitudes by approximately 46 days between Florida-North Carolina and Atlantic Canada (N.S.-N.B.). The time from larval metamorphosis to stream arrival increased from about 32 days south of Cape Hatteras to about 75 days in Atlantic Canada. This may reflect the narrow shelf zone in the south and the wide shelf zone off Atlantic Canada if metamorphosis occurs near the continental shelf edge.

The analysis of otolith daily age for anguillid larval/glass eels has been criticised due to the mismatch between the age at continental arrival and estimated spawning time and the spawning time estimated from larval length distributions in the spawning area (Cieri and McCleave 2000, Powles and Warlen 2002, McCleave 2008, Martin et al. 2010). Oceanic currents appear to have most American eel larvae join the Gulf Stream between Northern Florida and North Carolina (Kleckner and McCleave 1988, McCleave 1993). The otolith-based estimate of 46 days between coastal arrival in Florida-N.C. and Atlantic Canada (Wang and Tzeng 1998) is much less than half the 101 days based on mean dates of the middle of the elver run timings to the southern U.S. (February 11, based on Goose Creek, S.C. and Guana River Dam, FL) and Atlantic Canada (May 23, based on the Digdeguash River, N.B. and Gaspereaux Brook, N.S.) (Table 3). The otolith-based estimate of about 60 days for the migratory period between N.C. and Atlantic Canada (Powles and Warlen 2002, McCleave 2008) was also much lower than that based on observed run timing. Substantial differences in otolith-based estimates of glass eel ages from comparable sites occurred between studies (McCleave 2008). Elver run timing was later in the year in northern areas than in southern areas, as expected for larvae distributed from a southern point by the Gulf Stream, and the run duration decreased significantly with increasing latitude ($r = -0.60$, $p = 0.003$). Some glass eels undoubtedly arrive in northern coastal areas a week to more than a month before substantial entrance to streams occurs due to the gating effect of seasonal low water temperatures or high discharge (Jessop 1998, Jessop 2003b). However, the peak in run abundance to a stream remains fairly similar among years (Jessop 2003a). Although otolith daily age estimates for larval and glass eels may be inaccurate, the

relative duration of the estimated time to metamorphosis and of the post-metamorphic phase, in relation to latitude, may be plausible. At some ASMFC YOY sites, the run monitoring period may have underestimated the actual run period due to administrative issues.

Hormones, such as thyroid and cortisol, may control metamorphosis (Otake 2003), migration, and settling in glass eels (Edeline et al. 2004). Hormones are also genetically mediated, integrating both genetic and environmental influences as well as regulating gene transcription, neuronal, and metabolic activities (Dufty et al. 2003, Edeline et al. 2009). Transport across the continental shelf may be by directional swimming (FWS 2007, Miller 2009) in conjunction with selective tidal stream transport (STST) (Jessop et al. 2001).

Random timing of metamorphosis implies that the distribution of larvae/glass eel abundance to any particular geographic area is random. This could result in large geographic areas or those at range extremities, such as the Gulf of St. Lawrence, irregularly receiving recruitments that are either inadequate or excessive. It is also inconsistent with the hypothesis that the distribution and recruitment of glass eels/elvers is proportional to coastal watershed area whereby large watersheds receive recruitments proportional to their geographic area, with suitable habitat for eels presumed proportional to watershed area) (COSEWIC 2006). For two smaller Atlantic coastal rivers, Jessop (1998) found that elver recruitment was not proportional to watershed area. Recruitment, expressed as catch per net (CPUE) by the elver dip net fishery, varied regionally rather than being evenly or randomly distributed by geographic area and was greatly influenced by regional coastal oceanic current patterns. The

recruitment-geographic area hypothesis is also inconsistent with the observed high percentage of females (100% in the Lake Ontario - upper St. Lawrence River (LO-USLR)) (COSEWIC 2006) and the observation that low densities of juvenile eels results in high proportions of females (Krueger and Oliveira 1999, Tesch 2003, FWS 2007). The latter suggests that low recruitment to the St. Lawrence River area occurs relative to available habitat. Dutil et al. (2009) confirm relatively low glass eel abundance in the Gulf of St. Lawrence and that recruitment to regional rivers is substantially lower than to Atlantic coastal sites. Relatively greater distances from the spawning area, enroute mortality, or settlement might contribute to low juvenile recruitment relative to area for the Gulf of St. Lawrence and upstream areas of the St. Lawrence River. Cold surface temperatures in the Gulf of St. Lawrence during the larval/glass eel seasonal migration period may also contribute to reducing their recruitment. In-stream density effects on metagametic sex determination may be difficult to separate from other factors such as sex-linked upstream migration patterns or habitat choices (Davey and Jellyman 2005).

A similar phenomenon of relatively low recruitment to large northern geographic areas also occurs for the European eel (Dekker 2003). Recruitment differences also occur within smaller regions, such as between the western coast/Atlantic and eastern coast/North Sea regions in England and Wales (Bark et al. 2007). Stock abundance appears stable in western England and Wales and declining in eastern England. Stream populations also appear to be stable in western Scotland (Adams et al. 2013) where higher, more stable recruitment may occur due to its proximity to the continental shelf and regional current and wind conditions. Stock stability in the presence of declining recruitment in the Rio Esva (northwestern Spain) (Lobón-Cerviá and Iglesias

2008) and the River Fremur (Brittany) (Acou et al. 2011) has been attributed to density-dependent mortality.

American eel fecundity increases exponentially with size (McCleave 2001) while larval mortality increases roughly exponentially with drift duration (Bonhommeau et al. 2009). Female American eels from the LO-USLR area are the largest and most fecund in the continental distribution (Barbin and McCleave 1997, Tremblay 2009). Similarly sized female eels occur elsewhere in Atlantic Canada (Jessop 1987, Jessop et al. 2009, pers. comm. D. Cairns, Department of Fisheries and Oceans, Charlottetown, PEI) but comprise only a small portion of each river stock. However, the fecundity estimates for the LO-USLR area and St. Lawrence River and Gulf areas provided by Tremblay (2009) are higher relative to those for other areas provided by Barbin and McCleave (1997), Verreault (2002), and Wenner and Musick (1974). Regression slopes of fecundity on length are fairly similar in all studies but the adjusted means for the Tremblay (2009) estimates are higher. The fecundities at length provided by Verreault (2002) and Wenner and Musick (1974) may be substantially underestimated, perhaps due to differences in sampling and counting methods. Egg weight (size) also increases curvilinearly with increasing eel length and weight (Table 1, Tremblay 2009). The higher relative fecundity of smaller eels compared with larger eels results from the greater individual egg weight of larger eels (Tremblay 2009, COSEWIC 2012). Egg size may be positively related to the stage of female maturation. Larval size at hatching is proportional to egg size and increased larval size may result in greater survival (Ware 1975, Pepin 1991). However, the growth rate to a threshold size, and subsequently, may be as or more important than size per se (Cowan et al. 1996). Larger egg size

rather than higher fecundity in the LO-USLR area's large female eels may be a trade-off with implications for larval survival. The higher fecundity of the large eels from northern areas might simply compensate for duration-dependent enroute mortality of larvae. If it were equally advantageous on a population level for larvae of northern parentage to recruit to a southern continental area, as might occur under random larval distribution, then increased fecundity at size of northern eels might seem advantageous. However, if a high proportion of larval abundance is assumed to originate from spawners of LO-USLR origin (COSEWIC 2006), and larval distributional patterns are such that most larvae recruit to areas other than the LO-USLR area, there may be a biological advantage to the continental population. Any advantage to the LO-USLR stock in terms of recruitment is unclear.

Relatively low recruitment on a geographic area basis (but sufficient to better utilize available habitat, unlike the present situation in the LO-USLR and Gulf of St. Lawrence) may be the natural situation that creates the observed large size, high fecundity, and essentially female eel stock via the effects of density-dependent sex determination and local environmental effects on growth rate and size/age at maturity.

Regional contributions to the spawning stock have been hypothesized to be proportional to regional eel production area and relative fecundity, such that the Gulf of St. Lawrence and LO-USLR areas are believed to contribute substantially to the spawning stock (COSEWIC 2006) due to the large production area and high fecundity. Combining the recruit-geographic area and spawner-geographic area hypotheses implies that recruitment to a geographic area will be proportional to escapement from that area, with fecundity a regional constant. This hypothesis has not been accepted

because there is no evidence for the implied stock-recruitment relationship, which requires both a degree of non-random mating and larval dispersal if considered on a regional rather than a continental basis. The observation that animal dispersal and abundance typically declines with distance from an origin is also inconsistent with random abundance distribution and an assumption that recruitment to a large, distant, geographic area such as the Gulf of St. Lawrence might be proportional to its area or presumed high contribution to the spawning stock. Coastal distribution densities of glass eels/elvers differ widely along the Atlantic coast of Nova Scotia and the Bay of Fundy due to regional oceanic current patterns (Jessop 1998a). Evidence for non-random mating of the European eel and restricted gene flow among eels from three broad geographic groups (Mediterranean, North Sea and Baltic, and a northern (Iceland) group) was found by Wirth and Bernatchez (2001) based on highly polymorphic gene markers. This conclusion has been criticized on the basis that the findings really indicate a subtle temporal pattern rather than a spatial pattern due to unsynchronized sampling in northern and southern areas (Dannewitz et al. 2005, Pujolar et al. 2006, Maes et al. 2006, Palm et al. 2009). Evidence for panmixia has been found for the Japanese eel (Han et al. 2010, Minegishi et al. 2012) as well as against the theory (Tseng et al. 2006). Fundamentally, stock and recruitment on a continental basis must be related but the available information on spawner abundance and larval recruitment is inadequate for any analysis. The assumption of a stock-recruitment relation is the most precautionary approach (ASMFC 2012, ICES 2012). However, the analysis of time series of glass eel recruitment and river stock abundance in NW Europe indicate that substantial fluctuations in European eel recruitment are

relatively independent of stock abundance and that stock abundance varies much less than does recruitment (Knights 2011). Recruitment is correlated with cyclic oceanic climate factors (Miller et al. 2009, Durif et al. 2010) but there is no quantification of the oceanic climate effects on recruitment. Consequently, there is no evidence for a stock-recruitment relation at the observed levels of stock and recruitment. These conundrums can be resolved by an alternative hypothesis.

Phenotypic response to regional environmental conditions is the presumed explanation for the observed regional differences in American eel life history traits such as age and size at maturity. However, no comprehensive explanation exists of just how such environmental conditions control the phenotypic response. The temperature-size rule (TSR; an increased body size at maturation at lower developmental temperatures) is one hypothesis to explain the observed high phenotypic plasticity associated with geographic (latitudinal) variation in seasonal water temperatures and growth period. However, the TSR has no single comprehensive explanation. Different proximate mechanisms may operate in different species or at varying rates (Jessop 2010). Phenotypic responses are ultimately driven by gene expression which is governed by genetic variation (Fusco and Minelli 2010, Gagnaire et al. 2012).

The return of larvae and glass eels to any given parental latitude might occur via the timing of larval metamorphosis, duration of continental shelf migration, and seasonal constancy of the increased velocity of the Gulf Stream (Marchese 1999) which deliver glass eels to inshore waters over a relatively constant season (late winter-early spring) for any given latitude (Jessop 2010). The high fecundity of the large female eels from the LO-USLR area (Tremblay 2009), with fecundity increasing exponentially with size

(McCleave 2001), might help to balance the higher (roughly exponential) mortality experienced by larvae that drift for longer periods (Bonhommeau et al. 2009) to northern areas. Some compensatory reduction in mortality may occur with increased larval size. Elver recruitment to a river system may not be proportional to geographic area or discharge because of regional differences in elver recruitment (Jessop 1998a). Elver recruitment to small/moderate size Atlantic coastal streams may be more than required for their biological carrying capacity, contributing to the high mortality rate (≥ 0.995) experienced by elvers during the first summer of stream arrival (Jessop 2000). Eel mortality in freshwaters is density-dependent when elver numbers exceed a threshold value (Vøllestad and Johnsson 1988). Thus, the St. Lawrence River, at the northern end of the eel's distribution, may not receive elver recruitment proportional to its watershed area, discharge, or accessible habitat area, and presumed spawner escapement. This would be consistent with the hypothesized importance of the LO-USLR area under the assumption that the LO-USLR contributes substantially to recruitment elsewhere but also implies that the LO-USLR does not benefit as greatly from its own escapement, a conclusion difficult to accept. Other factors may be important if relative recruitment numbers are not primary.

The number of annual recruits required to support a stable population of older fish (LO-USLR mean age of silver eels about 21.5 years; Tremblay 2009) is less than for a similarly abundant population of younger fish (Chesapeake Bay silver eel mean age about 9 years; Owens and Gear 2003, Weeder and Hammond 2009). This is an argument in favour of fewer recruits to the LO-USLR than might be expected on the basis of rearing area or discharge.

Jessop (2010) has proposed a genetic link between larger elver size and older age at recruitment and larger female spawner maturation size with increasing northern latitude. Glass eel/elver recruitment occurs later in the year at northern latitudes than at southern latitudes and the converse is true for the timing of silver eel escapement (ASMFC 2012). The timing of larval metamorphosis may be controlled by an internal biological clock (Kulczykowska et al. 2010). The intrinsic circadian clock requires daily resetting by environmental cues such as light and temperature to ensure synchronization with the day-night cycle. Daylight hours increase with latitude during the growing and spawning season and water temperatures decrease (Jessop 2010).

The diel clock mechanism affects a variety of other gene expression regulatory networks. Many biological clock components are maternally inherited and present at a very early embryonic stage. Gonadal development in female eels begins one or more years after continental arrival as an elver (Davey and Jellyman 2005) and environmental imprinting may occur at that time. Consequently, the larval time of metamorphosis may be linked to the age of adult maturation via a phenotypic or genetic mechanism that has developed due to regional genetic diversity not detected by the analysis of neutral genetic markers typically examined by studies concluding genetic panmixia in anguillid eels (Jessop 2010). Thus, the older eels observed in northern waters would produce larvae that metamorphose at an older age thereby reaching the northern areas of their parentage (and perhaps with a degree of regional fitness), with analogous results over the geographic range of the eel. A genetically-based biological clock mechanism controlling the timing of larval metamorphosis and maternally inherited is not incompatible with the results of Gagnaire et al. (2012) provided that free recombination

occurs between metamorphosis triggering loci and local adaptation loci, consistent with the diversity of geographic patterns observed at selected loci.

Epigenetics is the study of heritable changes in gene expression and function that cannot be explained by changes in DNA sequence (Bossdorf et al. 2008). Recent evidence indicates that heritable variation in ecologically relevant traits (e.g., size at age, growth rate) can be generated via a suite of epigenetic mechanisms even in the absence of detected genetic variation, as with panmixia (Bossdorf et al. 2008).

Phenotypic plasticity may promote the origin of novel phenotypes, adaptive radiation, divergence among populations and species, and new species formation (Pfennig et al. 2010). Phenotypic variation can promote the accumulation and release of cryptic genetic variation expressed only under certain environmental or genetic conditions. The effect of plasticity on diversification may depend on the combined effects of the genetic structure, selection, and gene flow. The importance of epigenetic inheritance relative to genetic inheritance remains controversial, largely due to the relative scarcity of epigenetic studies (Bossdorf et al. 2008).

Quantitative genetic trait variation (Q_{ST}) at the among-population level is weakly correlated with and much higher than for neutral markers (F_{ST}). It may undergo divergent selection such that gene flow may be high enough to prevent differentiation of neutral markers but insufficient to prevent local adaptation of life history traits (Conover et al. 2006; Naish and Hard 2008). Neutral and adaptive genetic variation are typically uncoupled (Lynch 1996, Reed and Frankham 2001) and the apparent genetic homogeneity revealed by neutral markers, such as microsatellites, may be underlain by substantial heterogeneity in adaptive variation (Larsen et al. 2007, Hauser and Carvalho

2008). Anguillid eels are catadromous, but their genetic diversity is only slightly less than that of marine fishes (Tseng et al. 2006). The genetic diversity of American eel is of similar order to that of marine fishes (one SNP every 114 pb; P.-A. Gagnaire, pers. comm.). Measures of Q_{ST} are unavailable for anguillid eels, but their evaluation might support a degree of geographically distributed genetic structure in the presence of panmixia (Maes and Volckaert 2007). Measures of Q_{ST} are difficult to obtain because of the requirement for mating of eels with known genetic background and rearing under controlled conditions to separate genetic from environmental effects.

An analogous development has occurred in recent years in the concept of adaptive population structure in marine fishes (Hauser and Carvalho 2008). Many marine fishes once thought to lack genetic differentiation due to wide geographic distribution over a wide range of environments, extensive larval and adult dispersal, and large population size have been found to show population subdivision on limited geographic scales. Divergence in phenotypic traits, despite the lack of neutral genetic differentiation, has been interpreted as evidence for the adaptive significance of population structure (Hutchings et al. 2007). Similarities to the anguillid eel situation are notable.

The elver maturation biological clock hypothesis implies that a decline in spawner escapement from a given area, such as the LO-USLR, affects primarily recruitment to that area rather than having a wider effect on the continental stock. Consequently, improvements to the spawning escapement from the LO-USLR area would depend on increased regional stock abundance through better fish passage and reduced turbine mortality at hydroelectric dams such as the Beuharnois and Moses-Saunders dams,

and decreased fishing exploitation. The DFO (2010) report reviews the mitigation measures taken since the mid-1990s to reduce fishery exploitation, improve fish passage at some dams, and develop elver stocking programs for Lake Ontario and two Quebec sites. Genetic differences between the eel stock of the Gulf of St. Lawrence and St. Lawrence River regions and Atlantic coastal sites may make such stocking inadvisable (Bernatchez et al. 2011). This statement seems incompatible with the genetic homogeneity of panmixia and associated random distribution hypotheses so theories are proposed of non-random dispersal and differential survival associated with variation in individual genetic characteristics within a cohort of an otherwise panmictic population. Furthermore, if the Gulf of St. Lawrence/St. Lawrence River region has unique genetic characteristics and stocking is inadvisable, then the “rescue effect” hypothesis (COSEWIC 2006) cannot be counted upon to restore or maintain such unique characteristics. Rescue of this stock must then depend upon regional management actions to reduce local fishery exploitation and improve fish passage at dams. However, if the unique characteristics of the Gulf of St. Lawrence and St. Lawrence River large female eels also occur in the similarly large female eels found in much lower abundance throughout Atlantic Canada, then the rescue effect may be viable if these characteristics can be maintained in the population.

In summary, the panmixia hypothesis (random breeding) is well supported by the analysis of neutral genetic markers, although such analysis may not fully characterize anguillid eel genetics. The random distribution assumption seems deficient and calls into question interpretations of panmixia that assume random larval distribution. Further insight into anguillid eel genetics and larval metamorphosis and distribution is required.

The structure of habitat geographic zones (designatable units)

The COSEWIC (2006) report notes that “sub-speciation, geographic heterogeneity, range disjunction, or biogeographic distinction have not been demonstrated in the American eel population”, thus no consideration was given to assessment below the species level. The FWS (2007) report also found no basis for declaring the LO-USLR area as a Distinct Population Segment (DPS) under the Endangered Species Act for a similar reason. The studies by Jessop (2010), Côté et al. (2009), Bernatchez et al. (2011), and Gagnaire et al. (2012) suggest that the American eels in the Gulf of St. Lawrence and St. Lawrence River drainage area may have genetically unique growth rate characteristics that may merit special protection, even within the concept of panmixia. Coupled with the disproportionately low juvenile recruitment to the LO-USLR area and the stable glass eel/elver recruitment to Atlantic coastal areas of Canada and the U.S., it may be that a more appropriate status assessment would distinguish between the Gulf of St. Lawrence and St. Lawrence River drainage area and the remaining Canadian freshwater ecological areas (FEAs), as defined by COSEWIC (2006).

Justification for an elver fishery

The biological justification for an elver fishery in the Scotia-Fundy (now Maritime) Region of the Maritime Provinces, which began in 1989, was first presented in Jessop (1995) and further described in Jessop (1998a). An elver fishery is most justified where elver recruitment and density-dependent and finite mortality rates are high (>99%)

(Jessop 2000). These conditions may occur in many Atlantic coastal and Bay of Fundy streams. All estimates of elver mortality rate are high, ranging from instantaneous rates of 0.0015 to 0.0107-0.0233 for European eel elvers (cited in Jessop 2000) to 0.0612-0.0617 for American eel elvers, equivalent to finite mortality rates of 0.9945-0.9968 in the East River, Chester, N.S. Mortality rates may have been increased due to density-dependent mortality associated with cannibalism by faster growing YOY and high predation by larger eels, which are the dominant predatory fish species in the river (Jessop 2000). A common problem in Atlantic coastal N.S. where much of the fishery occurs is low stream pH. This may be a physiological stress factor and limit food supply due to lower productivity, thereby affecting growth rate (Jessop 2000) but may not be a direct mortality factor (Reynolds 2011, COSEWIC 2012). Annual fishery exploitation rates of 30-50% of the elver run may have little effect on the abundance of yellow and silver eel production when the mortality rate is high (Jessop 2000). Harvesting elvers in a given stream does not affect eel stocks in other nearby rivers because most elvers entering a river mouth move upstream at the pace (often a few 10s of meters per day in small coastal streams) permitted by environmental conditions (Jessop 2000, 2003b).

Since inception, the elver fishery has been tightly controlled by (a) limiting the number of licenses to nine, (b) restricting each licensee to a defined geographic area and approving fishing only in specific rivers within that area, (c) the prevention of elver fisheries in rivers with an existing fishery for larger eels, (d) restrictions on the type and quantity of fishing gear used, other than dip-nets, (e) a requirement to release alive any by-catch of other species, (f) an overall quota of 1000 kg per license (since reduced to 900 kg), with a limit of 300 kg from any river, and (g) submission of daily records of

catch and fishing effort by gear type. Although the price for elvers has varied greatly over the years, it has recently reached historic highs due to demand from the Asian aquaculture market in response to the European Union ban of eel exports and declines in catches of Japanese eel elvers. The value of the elver fishery has exceeded that for the traditional yellow and silver eel fisheries since about 1995 (Jessop 1995, 2000a), particularly at recent record high prices.

The economic benefits of fishing elvers versus larger eels depend on both the relative market values of each life stage and the survival rate from elver to silver eel (Chaput 1997). All eel fisheries occur on pre-spawners and spawners die after spawning. High elver recruitment and subsequent high density-dependent mortality rates favour an elver fishery.

The relative economic value of an elver fishery over that for yellow or silver eels can be estimated following Chaput (1997). For example, if we assume 6,500 elvers/kg with an elver fishery value of \$1,000/kg and a yellow eel harvest at 4 eels/kg valued at \$6.50/kg, the relative price differential (PD) becomes 10.56 and the survival rate which results in equal value of the fisheries (S_E) is 0.0947. If silver eels are harvested at 2 eels/kg, the PD = 21.13 and $S_E = 0.047$. Given an elver finite mortality rate of about 0.99 ($S_E = 0.01$) during the first year of continental arrival and additional annual mortality until harvested at perhaps 8-10 years old for yellow eels and 15-20 years for silver eels, it is clear that the cumulative lifetime survival rate must be less than 0.01.

Consequently, the elver fishery is many times more biologically justified than is a yellow or silver eel fishery. Fig. 1 of Chaput (1997) shows that if a yellow eel based PD of

10.56 and S_E of 0.01 is assumed, the economic value of the elver fishery should be about 10 times that of the larger eel fishery.

An alternative approach compares the reported landings and values of American eels taken in the freshwater and sea fisheries of eastern Canada with that of the elver fishery. In 2010, 61 tonnes of American eels valued at \$530,000 was reported landed by freshwater fisheries and 260 tonnes landed by sea fisheries, with no value given (Fisheries and Oceans Canada, Commercial Fisheries, www.dfo-mpo.gc.ca). Assuming an equal value/kg for freshwater and sea fisheries, the total catch in 2010 was 321 tonnes valued at \$2.26 million. This compares with a 2010 elver fishery catch of 1,573 kg valued at \$661,000. In 2011, the elver catch was 3,530 kg valued at \$6,870,000, illustrating the elver market volatility and the often favourable economic value of the elver fishery relative to the fishery for larger eels.

American eel status relative to European and Japanese eel

Historically, American eels have not been as heavily fished as European and Japanese eels, except perhaps in certain areas such as the LO-USLR and mid-Atlantic states/Chesapeake Bay. European and Japanese fisheries may allow fishing of all life stages (elver, yellow, silver eel) in a river system; in the U.S. and Canada, one or at most two stages are fished in any river system (ASMFC 2012). The declines in American eel catches from the 1980s onward followed a fishing-up and fishing-down effect as market demand increased in the 1960s (Robitaille et al. 2003, ASMFC 2012, p. 4) to supply European and Asian demand. European yellow/silver eel catches peaked in the late 1960s and began their decline during the 1970s while elver indices steadily

declined after about 1980 (Decker 2009). The stable Canadian elver indices since 1996 and American elver indices since 2000 suggest that American eel recruitment may not be as affected by the factors affecting European eel recruitment. Japanese eel catches for elvers, yellow, and silver eels have declined since about 1969 (Tsukamoto et al. 2009). The generally lower intensity of the fishery, particularly for American eel elvers, relative to that for European and Japanese eels, the large areas of habitat that are unfished in North America, and stable, if not increasing, elver recruitment indices suggests that the stock status of the American eel may be in a less serious condition than are the European and Japanese eel.

The proportions of unfished areas relative to fished areas in Europe, North Africa, and eastern Asia, are unknown but likely lower than in North America. The total habitat area for eels appears highest for Europe, followed closely by North America and then Asia with a much smaller area (Tesch 2007, Fig. 45). If habitat area is proportional to range coastline, then habitat areas for Europe (87,000 km², Moriarty and Dekker 1997) and North America (United States and Canada) might be fairly similar because Europe has a coastline length of about 89,000 km (CIA Factbook) as does that of eastern North America from Labrador to the Mexican border, including Lake Ontario, the St. Lawrence River, and Gulf of St. Lawrence ([infoplease](#), NRCan). Asia has a Japanese eel habitat coastline of about 50,000 km (FAO Japanese eel habitat map). The measured length of a coastline depends on the scale of measurement, increasing with decreasing scale, and various reported measurements may not all use the same scale. The comparability of these coastline measurements is believed to be reasonable. The relative eel

productivities of these regions are unknown but might be assessed by their relative commercial catches.

The timing of and declining trend in abundance for American, European, and Japanese commercial yellow and silver eel landings and of glass and yellow eel recruitment indices have been compared within and among species and correlated with potentially causative factors such as oceanic climate by a variety of studies, e.g. Bonhommeau et al. (2008), Miller et al. (2009), and Durif et al. (2010). Changes in the pattern of reported commercial landings of anguillid eels can be examined by the statistical method known as changepoint analysis (Killick and Eckley 2011). The process of identifying the optimal number and location of changepoints in a data series increases in difficulty with the length of the data series and may be both subjective (based on output plots) and statistical (based on different methods and assumptions about the nature of the data). The following changepoint analysis of temporal changes in mean landings was based on the exact search Segment Neighbourhood method, with adjustment of the penalty function used to examine alternative fits (Killick and Eckley 2011; Eckley et al. 2011). A cumulative sum (CUSUM) approach was used that assumed (based on normal probability plots) a non-normal data distribution. With increasing data set size, the problem of identifying the optimal number and location of changepoints increases. The choice of an appropriate penalty may be difficult because it depends on factors such as the size of the changes and segment length, which may be unknown prior to analysis. Assessment of the optimal number of changepoints was based on the “elbow” method and visual plot examination. The elbow method uses a maximum likelihood test statistic that produces a large difference for a “true”

change point and a small difference for a “false” change point. The optimal number of change points is indicated by the change (elbow) in the plot curve of the measure of fit of any particular number of change points against the number of change points considered. The principle of parsimony was applied.

The short-term (1950-2010) U.S. eel landings time series differs in several ways from the Canadian time series (Fig. 4). The U.S. landings data is more variable than is the Canadian data (U.S. coefficient of variation = 0.49, Canada = 0.35). Higher variability can result from factors such as differences in market forces, regional abundance, and completeness of statistics collection. Both time series show fairly high synchronicity in change point years but the decline in mean landings at the 1981-1982 change point was much greater for the U.S. than Canada, where landings remained relatively high until the early 1990s, after which a more sustained decline began. The first Canadian change point (1967) indicating an increased landings trend is earlier than for the U.S. (1973) and the period of mean peak landings (1967-1981) is longer than for the U.S. (1973-1982). The U.S. has a more rapid rate of decline during the 1980s and more extended period of low catch since the mid-1990s. The Canadian landings peak decline change point of 1981 is similar to that for the Moses-Saunders Dam yellow eel recruitment index (1981, Bonhommeau et al. 2008) and may be coincidental due to the pattern of eel landings, which began a sustained decline only during the 1990s. This may reflect a loose linkage between Canadian decreased landings, decreased spawner escapement, and ultimately reduced recruitment to the Moses-Saunders Dam. It may also imply a less significant effect of that recruitment on the national eel stock than on the regional eel stock. The strength of the relation between annual catch values and

trends and spawner escapement is controversial and may not be strong (ICES 2012). Reduced recruitment to the Moses-Saunders Dam and region would be expected to ultimately reduce spawning escapement from that region, modified in degree by any density-dependent survival which could buffer the relation between recruitment and regional standing stock. The U.S. and Canada/U.S. pooled landings peak decline change point of 1981 may be simply coincident and illustrative of the dominant effect of U.S. catches on the continental total. It is difficult to see such an immediate link between declining recruitment to the Moses-Saunders Dam and the decline in U.S. or continental landings.

American, European, and Japanese eel FAO reported landings (1950-2010) have all declined since their recent historical peaks but the timing of these peaks and degree of decline varies (Fig. 5). The peak mean reported landings of *A. anguilla* (1962-1976 average 18,271 t) was 8.8 times that for *A. rostrata* (1966-1981 average 2,068 t), and 6.1 times that for *A. japonica* (1957-1971 average 3,004 t). The catch of *A. japonica* was about 1.45 times that for *A. rostrata*. The Japanese and European eel declines in landings began in the early 1970s while North American catches began to decline in the early 1980s, first in the U.S. during the early 1980s and in Canada during the early 1990s (COSEWIC 2012; Fig. 4). Continental catch summaries blend regional differences. Prior to 1988, annual Asian catches were higher than for North America but have been lower since then due to a high rate of decline in Asian catches. To 2010, the decline from the mean peak catch has been about 82% for the Japanese eel, 61% for the European eel, and 52% for the American eel. The declines from peak to lowest catch are greater. The reliability of FAO catch statistics has been questioned,

particularly for Europe where landings reported by country may be unreliable and differ from those reported by FAO (Dekker 2003, Knights 2011, ICES 2012). The COSEWIC (2012) report provides annual DFO/NMFS (Department of Fisheries and Oceans/National Marine Fisheries Service) catch statistics for North America that average slightly higher (<5%) than for FAO, have greater variability, and differ somewhat in pattern and changepoints (Figs. 4, 5). For North America, we accept the DFO/NMFS landings data. The FAO catch values and trend for Japanese eel are similar to those reported for Japanese eels from Japan (Tsukamoto et al. 2009). It is clear that landings data time series may be problematic, as are the effects of market and regulatory changes that vary geographically and temporally. For example, increased aquaculture production in Europe since the late 1980s may have contributed to the decline in fisheries catch due to depression of market value, and thus commercial fishing effort, while total production has been maintained (Knights 2011). Additionally, the bias introduced into reported landings due to extensive stocking in southern Baltic countries, such as Germany and Poland, during the 1980-1990s is unknown but would tend to support higher landings in later years. European eel stocks, assessed by examination of river system time series rather than landings, have evidently not declined to the same extent as recruitment in recent decades and it is highly unlikely that the European eel is in danger of extinction (Knights 2011).

Long-term data on American commercial eel landings (Canada 1917-2010, DFO; United States 1880-2010, ASMFC) and European eel (1900-2000, Dekker (2003)) show substantial historic variability. The Canadian 1917-2010 time series clearly shows that two periods of peak mean landings have occurred over this time (roughly 1925-1939

and 1964-1993). Both peaks have been followed by sharp declines, suggesting that such levels of exploitation are unsustainable (Fig. 6). The longer U.S. time series (1880-2010) show three, if not four, peaks, each of which was followed by sharp declines. Peaks in national landings of comparable value occurred in the 1920s-1930s and 1970s-1980s in both Canada and the U.S. but the U.S. peaks were of a shorter, sharper period than in Canada. Historic declines in landings have also been followed by recoveries. However, the effects of factors such as market conditions and regional abundance during each event period are uncertain due to the absence of reliable catch-per-unit-effort information. The cause of the low landings in Canada and the U.S. in the 1920s and earlier is uncertain but might be due to earlier overfishing. The effects of potential overfishing in response to high market demand would be common to the post-1970s declines in Europe and North America but market and other conditions may have differed during the decline at the onset of World War II (Robitaille et al. 2003). Much of the decline in Canadian landings after 2004 may be due to the fishery management measures taken to reduce fishing effort and catch during the late 1990s and early to mid-2000s (DFO 2010). Comparison of the Canadian 1917-2010 and 1950-2010 time series shows similar changepoints, as do the U.S. 1880-2010 and 1950-2010 time series for the common periods.

Trends in European eel landings differ in several ways from those of American eel (Fig. 6). U.S. landings declined during the 1900s and were stable at a low level between the late 1900s and late 1920s. In contrast, European eel landings increased during the late 1900s and fluctuated at moderately high levels between the late 1900s and late 1920s. Landings in both Europe and North America increased during the late

1920s and 1930s. As previously noted, the decline in eel landings during World War II and their increase post-war are common to both continents, but the most recent decline in European eel landings began well before that for American eel in either the U.S. or Canada.

These historic relations among eel species may result from the interaction of regional eel habitat availability, habitat biological productivity, and fishery responses to market demand. The consistently higher catches of yellow/silver European eel than of Japanese or American eels reflects its large production area and high local demand (Ringuet et al. 2002). The much lower catch of American eels relative to European eels may result from lower local demand, preferences, and prices for imported eels in Europe and Asia to where much of the American eel catch is exported. Lower habitat productivity may also play a role, given that the eel production areas may be fairly similar. The pre-1988 higher catches of Japanese eels than of American eels may be due to both higher fishing intensity and probably higher habitat productivity in Asia despite a lower habitat production area. The post-1988 more rapid and severe decline may reflect the cumulative effect of intense fishing pressure on both glass eels and yellow/silver eels (Ringuet et al. 2002),

The timing and extent of yellow/silver eel catch peaks and subsequent declines for Japanese, European, and American eels is consistent with a fishing-up effect for yellow/silver eels with the decline beginning first for Japanese eels (peak catch 1969, changepoint 1971; Fig. 5) and closely followed by European eels (peak catch 1968, changepoint 1970 or 1976, depending upon whether the FAO or Dekker (2003) time series is used). At this time, rising economic prosperity stimulated the existing

Japanese and European preference for adult eels. The decline in European eel catches was followed by the decline in American eel catches (FAO peak catch 1975, changepoint 1979; DFO/NMFS peak catch 1978, changepoint 1981), first in the U.S. then in Canada, as fishing effort was increased in the 1960s (Robitaille et al. 2003) to meet European demand. Prior to the decline in Japanese large eel landings, Japanese eel aquaculture was increasing, first in Japan and Taiwan and later in China, which became a major producer in the 1980s (Ringuet et al. 2002). The decline in European large eel landings during the 1970s was followed by an increase in aquaculture during the late 1980s (Knights 2011). The high exploitation of glass eels for aquaculture in Asia and later Europe was followed by declines in glass eel harvest. Declining regime shifts in glass eel/yellow eel recruitment followed those for yellow/silver eel commercial landings, occurring in 1982 for European eels (6 - 12 years later than for yellow/silver eels, depending upon time series used), 1977 for Japanese eels (6 years later), and 1981 for American eels (0 years later) (Bonhommeau et al. 2008). The trend turning points estimated by the two methods are consistent, except for the American eel, in that a reduction in recruitment might be expected after a reduction in spawning escapement inferred by peak catches. For the European and Japanese eel, the changepoint declines for the commercial catches and glass eel indices are separated by a timespan similar to the mean age of female silver eels of each species, approximately 11-12 years for European eels (Knights 2011) and 7-8 years for Japanese eels (Kotake et al. 2005). The absence of such a difference for American eels is puzzling and may indicate that the Moses-Saunders Dam yellow-eel index is not a reliable indicator of continental recruitment. When only Canadian eel landings are considered, the Moses-

Saunders Dam eel index 1981 decline in mean recruitment (Bonhommeau et al. 2008) precedes the decline in Canadian eel landings by 13 years, which is approximately half the mean age (22 years) of female silver eels in Canada (COSEWIC 2012). This phenomenon is opposite that observed for European and Japanese eels. Declining recruitment to the Moses-Saunders Dam may have contributed to later declines in Canadian catches via the reduction in production of larger eels from the area upstream of the dam.

The growth of the eel aquaculture industry outside of Japan in Taiwan and China since the 1990s increased the demand for imports of glass eels, particularly from Europe and North America. The European export demand competed with the European eel aquaculture industry and natural habitat stocking programs. Exports were facilitated by the growing availability and cost effectiveness of air transport. The higher level of exploitation of both yellow and silver eels and elvers in Asia, followed by Europe, relative to that in North America has probably contributed importantly to the observed degrees of decline in the respective fisheries. Europe and Japan consume the regional production (wild catch and aquaculture) of yellow/silver eel products while yellow/silver eel products from North America are primarily exported to Europe and glass eels/elvers go to Asia, primarily China and Taiwan.

The approximate synchronicity of declines in recruitment for the three temperate eel species (10 year difference between Japanese eel and American eel, 5 – 10+ years between European and American eels, depending upon whether FAO or other data sets are used) has been attributed to common factors such as ocean warming (Knights 2011, COSEWIC 2012). Oceanic factors affecting larval survival probably act in

conjunction with anthropogenic continental factors such as overfishing, habitat loss and degradation, pollution, etc., but their relative importance in the decline of temperate zone anguillid eels remains uncertain (Miller et al. 2009). No quantification has been made of any relation between spawning success or larval survival and recruitment and oceanic environmental effects nor has such correlation or quantification been made for anthropogenic factors with observed trends in recruitment or stock abundance (Knights 2011).

Certain oceanic effects such as variability in marine production related to climate cycles or current systems (Miller et al. 2009) might be expected to affect the much longer migratory path of the European eel to a greater extent than that for the American eel. The occurrence of generally positive correlations between glass eel indices and the NAOI (North Atlantic Oscillation Index) for American eels and negative relations for European eels and the generally long duration of each phase of the NAOI (it has been mainly positive since 1980) (Côté et al. 2012) imply that oceanic environmental conditions have affected North American eel recruitment less than European eel recruitment since the 1980s. Infection by the swimbladder parasite *Anguillicolloides crassus* may reduce the speed and sustainability of swimming by migrating silver European eels (van Ginneken et al. 2005, Palstra and van den Thillart 2010). For American eels, the migration distance is less than half that and infections may have a proportionately lesser effect. This parasite was first discovered in North America in 1995 (Moser et al. 2001) and rapidly spread along the Atlantic coast of North America and into Atlantic Canada by about 2007 (Aieta and Oliveira 2009) and, presumably by elver stocking, into Lake Ontario by about 2012. This period post-dates the decline of

eels in the LO-USLR but its current presence may have uncertain effects on American eel survival and stock recovery.

Long-term cycles have occurred in American and European eel stocks, to the degree that stock abundance is reflected in reported landings (ASMFC 2012, Dekker 2003), and landings values similar to current low values have occurred in the past. A fisheries-independent index on a stock of European eels largely unaffected by fishing effort also shows abundance cycles that are correlated with oceanic environmental conditions (Durif et al. 2010). Thus, such fluctuations must, to some degree, be regarded as typical. On paleontological time-scales, large fluctuations in habitat area and presumably eel density have occurred in Europe (Kettle et al. 2008) and undoubtedly in North America in response to glaciations. The absence of eels in eastern Canada and along much of the United States Atlantic coast during the most recent glaciation about 10,000 years ago did not result in extinction of the American eel and it is difficult to conclude that current habitat losses, despite potentially serious effects on current abundance, pose a threat of extinction.

The available evidence supports a conclusion that the American eel stock has not declined as much as have European and Japanese eel stocks. American eel elver recruitment has been relatively stable since the 1990s in most areas, unlike the more continuous declines in European and Japanese glass eel indices.

Stock recovery actions

Even if oceanic factors are important, management actions are only feasible during the continental life stages. Although often disproportionately targeted due to

their ease of control, not all of the burden of stock recovery should fall on the commercial fisheries. Recent changes in fishery management regulations in Canada and the U.S. to reduce the number of licenses, increase minimum size limits, restrict fishing seasons, etc. (DFO 2010, ASMFC 2012) have not been matched by provisions to improve fish passage, both upstream and downstream, at more than a few of the many hydroelectric dams obstructing potential eel habitat (Busch et al. 1998, Verreault et al. 2004, COSEWIC 2012). For example, on the Saint John River, no provision for the upstream or downstream passage of eels exists at the Mactaquac Dam, the furthest downstream of the four large hydroelectric dams in the watershed. Few, if any, eels are passed upstream of the Mactaquac Dam incidental to the gaspereau (alewife and blueback herring) trapping and trucking operation. The dam is otherwise impassable to American eels and the species can be considered essentially exterminated from upriver of the dam. An historic, successful eel fishery operated in the Meduxnekeag River area (Eales 1968, Ingraham 1999) but declined gradually following the construction (1968 completion) of the Mactaquac Dam until its closure for fishery regulation reasons in the mid-1990s. Eels collected in the final year of the fishery would be a minimum of about 25 years old.

The difficulty (cost, feasibility, time to implement, etc.) of increasing habitat availability in the LO-USLR area by improving upstream and downstream fish passage at dams, particularly hydroelectric dams, has been well examined by MacGregor et al. (2010). Implementing some of these measures may take 40 years or more and they will only be achieved if strong action by provincial and federal regulatory agencies is taken. Such actions would allow for improvements in stock abundance many times greater

than further controls on the fishery or even its elimination. Furthermore, we believe that the latter actions would be unjustified, particularly given our contention that the continental stock is not endangered but is stable at a level lower than historic highs. As previously discussed, this contention is based on: (a) the stable or recently increasing catch trend of the ASMFC YOY indices at 13 of 16 sites over the past 12 years; (b) yellow eel indices that are variable but show no consistent trend and are essentially stable for the past 20 years at a level lower than the historic peak in the mid-1980s; (c) the stable but recently increasing elver index at the East River, Chester, N.S.; (d) the recent record high catches and high CPUE for the Maine elver fishery; and (e) the high catches and unusually rapid capture of quotas by many of the Canadian elver fishers in the past two years.

The management goal of rebuilding eel abundance to the levels observed in the mid-1980s (DFO 2010, COSEWIC 2012) may be unrealistic where fish passage issues dominate fishery issues. The eel abundance represented by the reported historic landings is unknown and likely varied over time. Just how future eel abundance would be assessed over the Canadian range is unclear. The mean landings during the mid-1980s (say 1983-1987) of 920.7 t is fairly similar to that of the changepoint analysis mean landings of 917.8 t for the 1981-1997 period and of the 991.6 t for the 1930-1938 period. Landings sharply declined after both peak periods, suggesting that the abundance represented by such landings is unsustainable if fishing occurs at such high levels. A more sustainable annual fishery catch level and a better definition of the stock recovery goal are required.

Summary

In summary, we believe that the available evidence provides no justification for the COSEWIC (2012) report to increase the threat level status of the American eel from “of special concern” to “threatened” and urge that the status level be revised to its previous level.

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Table 1. Estimated surface area for American eel growth habitat in freshwater and estuarine/coastal zones for Canada and the United States. U.S. nearshore habitat is assumed equivalent to Canadian estuarine-coastal sheltered/semi-exposed habitat.

Country	Region	Zone	Area (km ²)	Reference
Canada	Upper St. Lawrence R. – L. Ontario	freshwater	5,800	Verreault et al. 2004
	Ottawa River		3,700	Verreault et al. 2004
	Richelieu R. – Lake Champlain		1,200	Verreault et al. 2004
	Other		1,440	Verreault et al. 2004
	Downstream of dams		1,940 ^a	
	Total		14,080	
	St. Lawrence R. estuary and Gulf	estuarine- coastal	32,940	Cairns et al. 2012
Total Canada	freshwater - estuarine	47,020		
United States	Atlantic coast – Gulf of Mexico	freshwater	20,540 ^b	
	North Atlantic	nearshore	5,379	FWS 2007
	Mid-Atlantic		20,298	FWS 2007
	South Atlantic		12,172	FWS 2007
	Gulf of Mexico		30,604	FWS 2007
	Total	nearshore	68,453	FWS 2007
	Total U.S.	freshwater-nearshore	88,993	
Total Canada-U.S.		136,013		

^aEstimated as 16% of dammed area based on Busch et al. (1998) estimate for dammed area in U.S. No estimates are available for dammed freshwater areas in Atlantic Canada.

^bEstimated assuming U.S. freshwater/estuarine proportions are similar to Canadian proportion of 30% freshwater. A similar area estimate can be based on U.S. estimated freshwater stream habitat of 556,801 km (Busch et al. 1998) with average stream width of 37 m.

Table 2. Relative egg production by region and habitat (Fw = freshwater; estuarine in Canada is equivalent to estuarine/coastal in U.S.) for American eels based on a latitude – eNPP (effective net above ground primary production ($\text{g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$) during the growing season) relation from data in Huston and Wolverson (2011).

Region	Habitat	Area (km ²)	Latitude °N ^a	eNPP ^b	Weighted eNPP	Proportion female ^c	Length (mm) ^d	Fecundity ^e × 10 ⁶	Relative egg Production ^f	% of total
LO-USLR	Fw	5,800	44.4	139.6	1.13	1.0	935	13.6	89,091	15.7
Canada	Fw/estuarine	47,080	48.0	132.2	1.07	0.978	802	6.7	329,961	58.1
U.S.	Fw	20,540	35.6	136.8	1.11	0.655	674	4.8	71,325	12.6
N. Atlantic	Estuarine/coastal	5,379	43.8	140.4	1.13	0.655	594	3.3	13,132	2.3
Mid-Atlantic	Estuarine/coastal	20,298	38.4	140.3	1.14	0.655	660	4.5	67,912	12.0
S. Atlantic	Estuarine/coastal	12,172	30.7	126.8	1.03	0.655	577	3.0	24,701	4.4
Gulf of Mexico	Estuarine/coastal	30,604	29.4	123.6	1.0	0.655	577	3.0	60,538	10.7
Total U.S.		68,453							237,608	41.9
Canada + U.S.		136,013							567,569	100

^aMean latitude for a region.

^bEstimated mean eNPP at the mean latitude of a region based on data in Huston and Wolverson (2011), Supplement 5 for longitude range -55 to -85 °W and latitudes north of the equator based on the polynomial relation: mean eNPP = $-0.0039 \text{ Lat.}^3 + 0.3066 \text{ Lat.}^2 - 5.4063 \text{ Lat.} + 116.63$.

^cBased on Table 3, COSEWIC (2006).

^dBased on data in Table 2, COSEWIC (2006) and Table 2.2, ASMFC (2012); U.S. Fw length based on river sites.

^eBased on equations in Tremblay (2009), Table 3 for upper St. Lawrence River and Barbin and McCleave (1997) for the remaining regions.

^fBased on equation: area × weighted eNPP × proportion female × fecundity.

Table 3. Latitudinal distribution of run period and duration for American eel elvers for sites along the Atlantic coast of North America.

Site	Latitude °N	Run period	Run days	Reference
Petite Trinite R., PQ	49.53	June 15 - July 30	45	Dutil JD, M Michaud, A. Giroux 1989. CJZ 67:182-188
Digdeguash R., NB	45.18	May 6 - June 9	35	Jessop, B.M. 1998. CJZ 76: 2172-2186
Gaspereaux Bk., Guysborough, NS	45.03	Apr 30 - June 7	39	Jessop, B.M. 1998. CJZ 76: 2172-2186
East R., Sheet Hbr, NS	44.95	May 22 - July 15	55	Jessop, B.M. 2003. AFS Symp. 33: 17-36 (average of 4 yrs)
East R., Chester, NS	44.59	May 13 - July 15	64	Jessop, B.M. 2003. AFS Symp. 33: 17-36 (average of 4 yrs)
Mersey R., NS	44.04	Apr 28 - June 10	44	Jessop, B.M. 1998. CJZ 76: 2172-2185 (average of ERC and Argyll R.)
Meteghan R., NS	44.22	Apr 20 - June 3	45	Jessop, B.M. 1998. CJZ 76: 2172-2186
West Hbr Pond, ME	43.85	Apr 10 - June 14	67	ASMFC YOY database 2006
Jones R., MA	42.01	Apr 2 - May 21	50	ASMFC YOY database 2006
Annaquatucket R., RI	41.53	Apr 20 - June 26	68	ASMFC YOY database 2006 (average of 2004-2005)
Gilbert Stuart Bk, RI	41.52	Apr 11 - June 7	58	ASMFC YOY database 2006 (average of 2000-2005;2003 missing)
Connecticut R., CN	41.27	Feb 23 - May 25	92	ASMFC YOY database 2006 (average of 2000-2005)
Patcong Ck, NJ	39.31	Feb 8 - Apr 30	83	ASMFC YOY database 2006 (average of 2000-2006)
Millsboro Dam, Indian R. DE	38.59	Jan 15 - Apr 10	87	ASMFC YOY database 2006 (average of 2000-2005)
Turville Ck, MD	38.37	Mar 11 - May 22	73	ASMFC YOY database 2006 (average of 2000-2005)
Kamps Millpond, Rappahannock R., VA	37.75	Mar 25 - May 4	41	ASMFC YOY database 2006 (average of 2001-2005)
Brackens Pond, York R., VA	37.25	Mar 4 - May 31	89	ASMFC YOY database 2006 (average of 2001-2005, 2002 missing)
Warehams Pond, James R., VA	37.22	Mar 8 - May 17	71	ASMFC YOY database 2006 (average of 2003-2005)
Wormly Ck, York R., VA	37.22	Feb 22 - May 17	86	ASMFC YOY database 2006 (average of 2002-2005)
Black Ck, NC	34.77	Jan 22 - Mar 15	53	ASMFC YOY database 2006 (average of 2001-2005, 2003 missing)
Goose Ck, SC	32.91	Jan 8 - Mar 24	76	ASMFC YOY database 2006 (average of 2000-2005)
Guana R. Dam, FL	30.02	Jan 2 - Apr 2	91	ASMFC YOY database 2006 (average of 2001-2005)

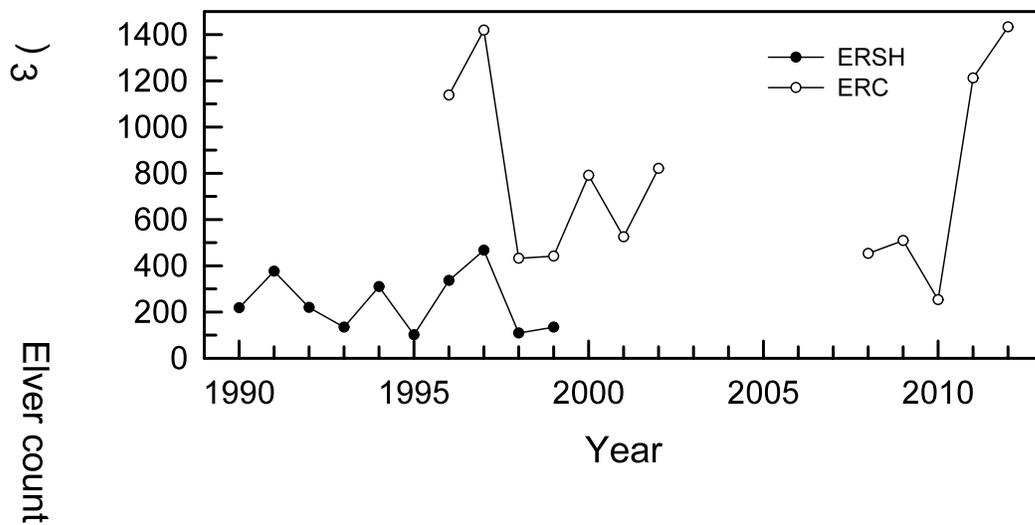


Figure 1. Annual counts of American eel elvers at the East River, Sheet Harbour (ERSH) and the East River, Chester (ERC), 1990 to 2012.

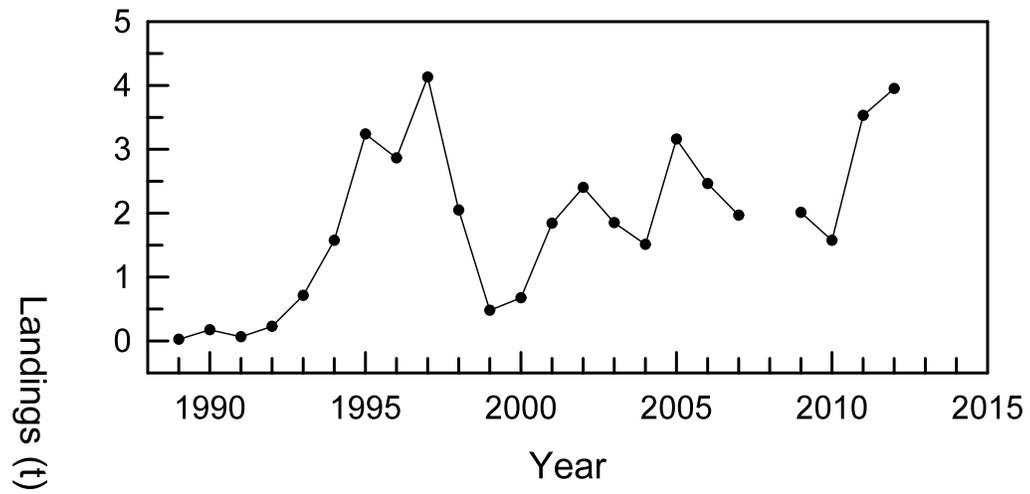


Figure 2. Commercial fishery landings of American eel elvers from the Maritime Region, Atlantic Canada, 1989 to 2012. Data unavailable for 2008.

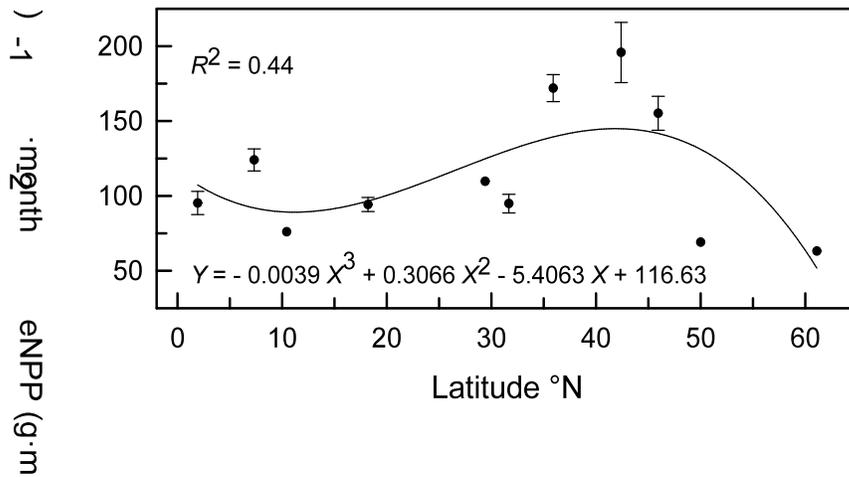


Figure 3. Mean (\pm 95% CI) eNPP (ecologically relevant continental net primary production) variation with latitude based on Huston and Wolverton (2011). Data are from sites in the range -55 to -85 °W longitude, approximately the range of rivers running to the Atlantic coast of North America. Confidence intervals (CI) are given only for means with $n \geq 3$; n range = 1-25.

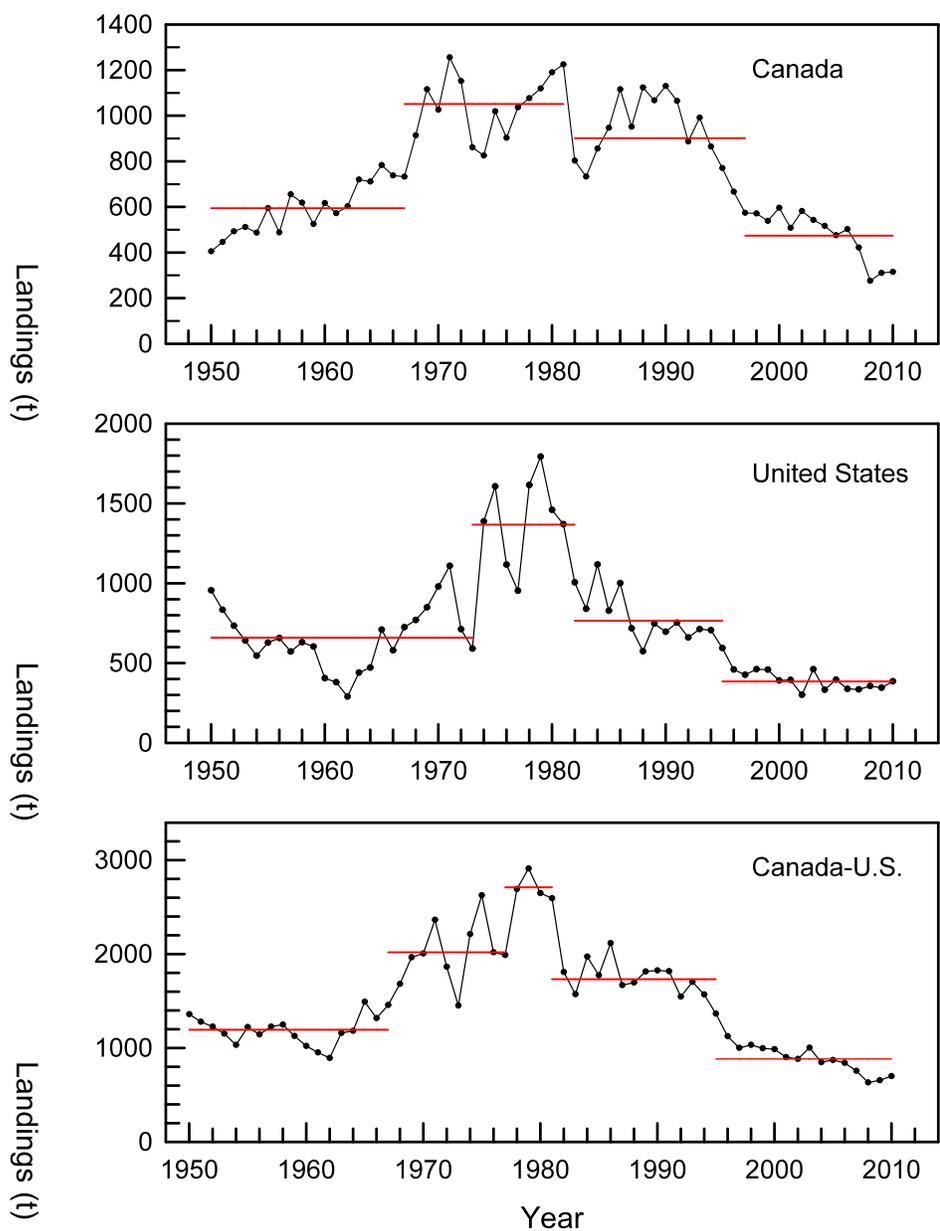


Figure 4. Reported landings (t) of American eels in Canada, the United States, and Canada-U.S. combined for the years 1950-2010 by the Department of Fisheries and Oceans and National Marine Fisheries Service. The horizontal lines represent changepoint mean landing values, with a significant changepoint occurring between means. Changepoint means and years are: Canada: 594.3, 1967; 1051.4, 1981; 901.1, 1997; 473.6; United States: 658.6, 1973; 1,367.3, 1982; 764.8, 1995; 384.9; Canada –

United States: 1,194.2, 1967; 2,018.2, 1977; 2,711.7, 1981; 1732.3, 1995; 882.5.

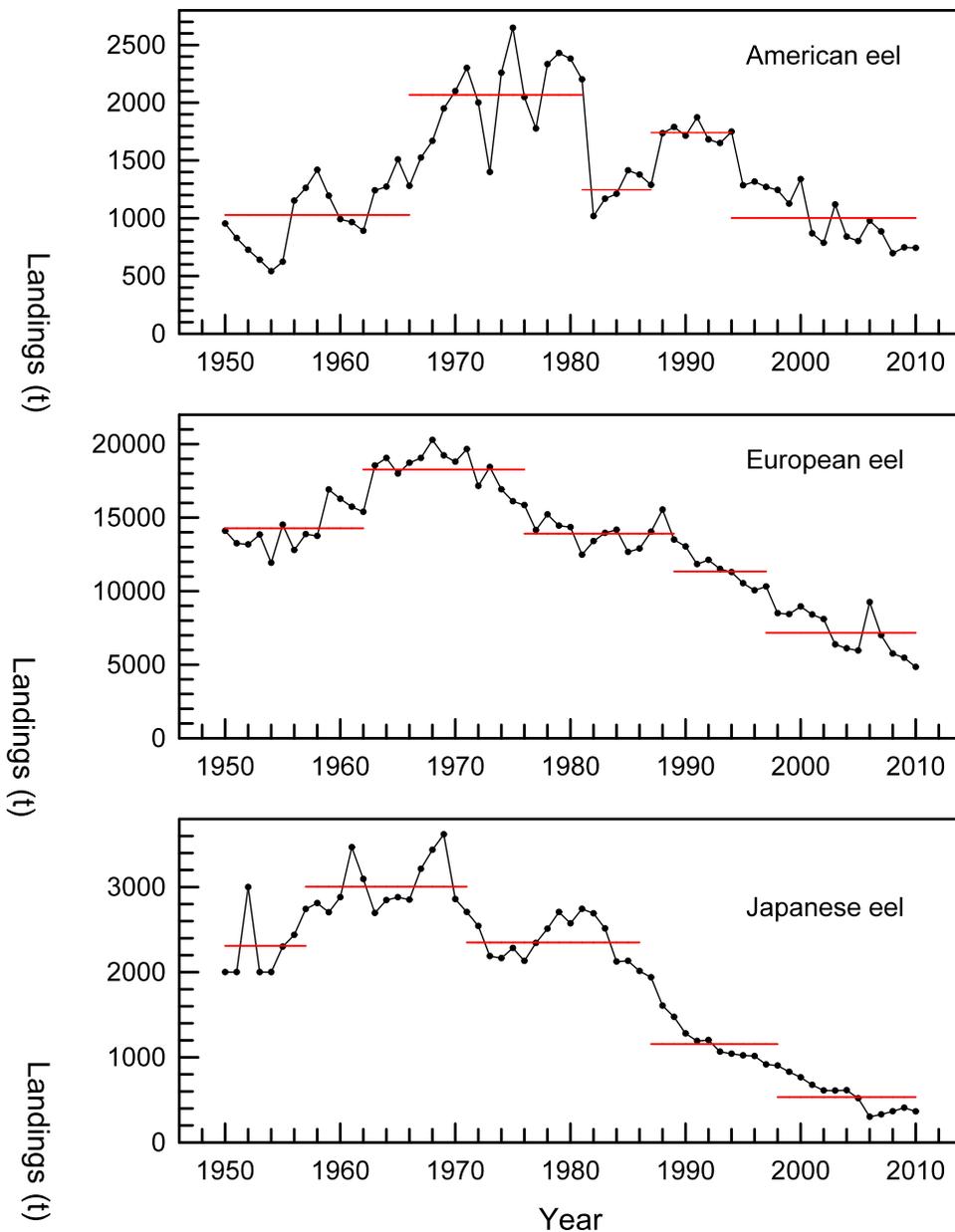


Figure 5. FAO reported landings (t) of American, European, and Japanese eels for the years 1950-2010. The horizontal lines represent changepoint mean landing values, with a significant changepoint occurring between means. Changepoint means and years are: American eel: 1,028.7, 1966; 2,068.0, 1981; 1246.0, 1987; 1741.4, 1994; 1,002.8; European eel: 14,272.8, 1962; 18,271.5, 1976; 13,908.9, 1989; 11,338.6,

1997; 7,163.1; Japanese eel: 2,310.1, 1957; 3,004.6, 1971; 2,350.4, 1987; 1,156.6, 1998; 532.8.

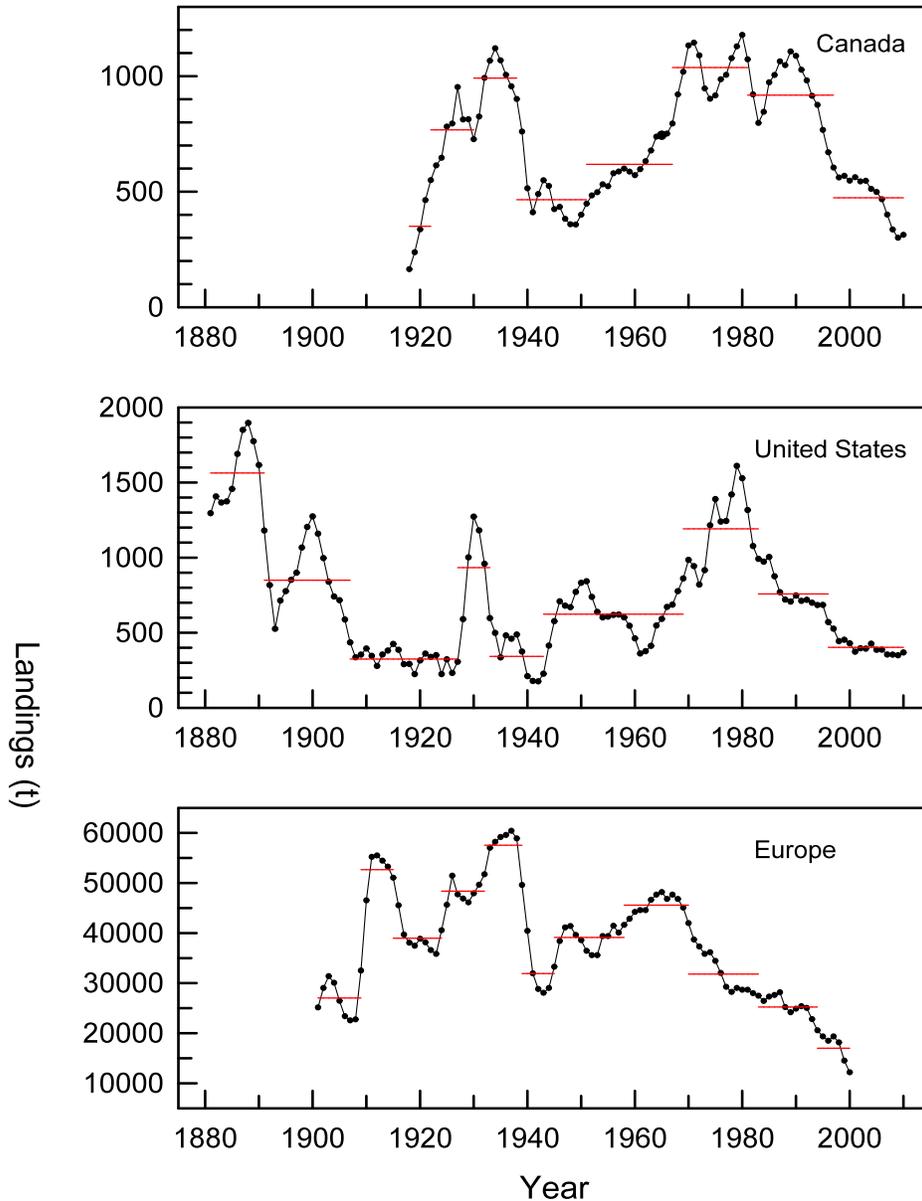


Figure 6. Long-term Anguillid eel commercial fishery landings (t) from Canada (1917 – 2010), the United States (1880 – 2010), and Europe (1900 – 2000), smoothed by a 3-year moving average. Changepoint means and years are: Canada: 350.2, 1922; 767.5, 1930; 991.6, 1938; 465.5, 1951; 618.2, 1967; 1037.0, 1981; 917.8, 1997; 473.6; United States: 1536.8, 1891; 849.8, 1907; 325.1, 1927; 933.2, 1933; 342.6, 1943; 623.3, 1969; 1192.1, 1983; 758.6, 1996; 402.6; Europe: 27,027.8, 1909; 52,662.1, 1915; 38,966.1,

1924; 48,385.5, 1932; 57,549.6, 1939; 31,921.3, 1945; 39,121.7, 1958; 45,578.7, 1970;
31,822.2, 1983; 25,230.0, 1994; 16,966.7.