Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

Canadian Science Advisory Secretariat (CSAS)

Research Document 2013/132

Central and Arctic, Gulf, Quebec, Newfoundland and Labrador, and Maritimes regions

Recovery Potential Assessment for the American Eel (*Anguilla rostrata*) in eastern Canada: functional description of habitat

T.C. Pratt[1], R.G. Bradford[2], D.K. Cairns[3], M. Castonguay[4], G. Chaput[3], K.D. Clarke[5], and A. Mathers[6]

[1] Fisheries and Oceans Canada
1219 Queen St E, Sault Ste. Marie, Ontario, P6A 2E5

[2] Fisheries and Oceans Canada
PO Box 1006, Dartmouth, Nova Scotia, B2Y 4A2

[3] Fisheries and Oceans Canada
P.O. Box 5030, Moncton, New Brunswick, E1C 9B6

[4] Fisheries and Oceans Canada
PO Box 1000, Mont-Joli, Quebec, G5H 3Z4

[5] Fisheries and Oceans Canada
P.O. Box 5667, St. John’s, Newfoundland and Labrador, A1C 5X1

[6] Ontario Ministry of Natural Resources
RR 4, Picton, Ontario, K0K 2T0

February 2014

Foreword

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Pratt, T.C., Bradford, R.G., Cairns, D.K., Castonguay, M., Chaput, G., Clarke, K.D., and Mathers, A. 2014. Recovery Potential Assessment for the American Eel (*Anguilla rostrata*) in eastern Canada: functional description of habitat. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/132. v + 49 p.

TABLE OF CONTENTS

ABSTRACT

This document provides a review of the habitat requirements of the American Eel (*Anguilla rostrata*), with a focus on habitat needs by life stage, estimation of the amount of habitat currently available and currently inaccessible for eels, determination of whether habitat will be limiting if recovery objectives are reached, assessment of how different habitats influence eel biology and carrying capacity, and finally addresses whether American Eel habitat usage may meet the requirements of a residence as defined by the *Species at Risk Act*. The American Eel has a complex life cycle, spanning oceanic, nearshore coastal, estuarine and freshwater environments. Little is known about habitat requirements for migrating, spawning, egg and leptocephali (larval) stages in the ocean. After metamorphosis into glass eels, ingress into nearshore coastal, estuarine or freshwater is linked to diurnal and lunar cycles. During the inland migration and growth stage as elvers and yellow eels, respectively, water velocity and temperature, and substrate become more important habitat features. More than most fishes, American eels are influenced by their habitat because of the relationship between their highly variable life history characteristics and habitat features, including habitat-mediated impacts on growth and sex determination. The distribution of the American Eel covers a vast geographic area, and at current abundance levels, habitat is not thought to be limiting across most of its range. However, there are specific locations in northeastern North America where access to substantial quantities of habitat have been lost due to barriers; as much as 84% of freshwater habitat may be currently inaccessible. It is uncertain whether these habitat losses are sufficient to limit recovery. Overall, given the wide distribution of the species, localized areas of reduced habitat quantity and quality in either freshwater or marine areas are not likely to constrain the possibility of species recovery.

Évaluation du potentiel de rétablissement de l'anguille d'Amérique (*Anguilla rostrata*) dans l'est du Canada : description fonctionnelle de l'habitat

RÉSUMÉ

Le présent document porte sur l'examen des besoins de l'anguille d'Amérique (*Anguilla rostrata*) en matière d'habitat et met l'accent sur chaque stade biologique et sur l'estimation de la superficie d'habitat actuellement disponible et inaccessible pour les anguilles. Le document analyse si l'habitat sera limitatif si les objectifs de rétablissement sont atteints, fournit une évaluation de la manière dont différents habitats ont une incidence sur la biologie et la capacité biotique de l'anguille, et, enfin, indique si l'utilisation de l'habitat par l'anguille d'Amérique peut respecter les exigences d'une résidence conformément à la définition de la *Loi sur les espèces en péril*. L'anguille d'Amérique a un cycle biologique complexe qui se déroule dans les milieux océaniques, côtiers, estuariens et d'eau douce. On connaît mal ses exigences en matière d'habitat aux stades de la migration, du frai et du développement des œufs et des larves leptocéphales dans l'océan. Après leur métamorphose en civelles, les individus se dirigent vers les milieux côtiers, estuariens ou d'eau douce en fonction des cycles lunaires et diurnes. Au cours de la migration des civelles vers les terres et du stade de croissance d'anguille jaune, la température et la vitesse de l'eau ainsi que le substrat deviennent des caractéristiques de l'habitat plus importantes. Plus que la plupart des poissons, l'anguille d'Amérique est régie par son habitat en raison de la relation entre les caractéristiques très variables de son cycle biologique et des composantes de l'habitat, notamment des incidences qu'à l'habitat sur la croissance et la détermination du sexe. L'anguille d'Amérique est répartie dans une vaste zone géographique et, selon les niveaux d'abondance actuels, l'habitat ne devrait généralement pas être limitatif. Toutefois, il y a certains endroits dans le nord-est de l'Amérique du Nord où l'accès à de nombreux habitats a été perdu en raison d'obstacles; ainsi, plus de 84 % de l'habitat en eau douce seraient ainsi devenus inaccessibles. On ne sait pas si ces pertes d'habitat seront suffisamment importantes pour limiter le rétablissement. Dans l'ensemble, étant donné la répartition étendue de l'espèce, la réduction de la superficie et de la qualité des habitats de certaines zones locales, tant dans les zones marines que d'eau douce, n'est pas susceptible de limiter les possibilités de rétablissement de l'espèce.

INTRODUCTION

American Eel (*Anguilla rostrata*) has one of the most complex life histories of any North American fish. It is semelparous, tolerates a wide range of temperatures and salinities, and exhibits facultative catadromy (Tesch 2003). Found in coastal, brackish and freshwater systems from Venezuela to Greenland, eels from across this wide geographic range are panmictic (comprise a single breeding population; Gagnaire et al. 2012). Spawning-phase silver eels migrate to the Sargasso Sea to spawn and subsequently die after spawning. The spawning location is inferred from the distribution of larvae sampled at sea as spawning has not been observed. Larval stage leptocephali drift on oceanic currents for up to one year reaching approximately 60-80 mm in length, after which they reach continental waters and metamorphose into glass eels. Glass eels initiate feeding, becoming progressively more pigmented and are termed elvers. After a few months they become fully pigmented and are referred to as yellow eels. The yellow eel stage can last from 4 to over 25 years, with freshwater residency times generally increasing with increasing latitude. Preceding the initiation of the spawning migration a final metamorphosis event occurs and eels transition into the sexually mature, non-feeding silver eel phase. The American Eel is sexually dimorphic in growth, maturation, and distribution, with females growing larger and maturing later than males. Males are more commonly produced in southern latitudes, while the reverse is true for females; this may be due to more lacustrine habitat available in the northern part of the species range.

A precipitous 99% decline in juvenile American eels ascending into Lake Ontario, near the northern end of the species' range, was recorded between 1983 and 2000, which led to concerns about their persistence in St. Lawrence River watershed, and at the time of the decline, about the viability of the species as a whole. Due to genetic evidence confirming the panmictic nature of American Eel, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) determined that there was one Designatable Unit of the species in Canada. As a result of these declines, the American Eel was assessed as Threatened by COSEWIC. When COSEWIC assesses an aquatic species as Threatened or Endangered, the Minister of Fisheries and Oceans Canada (DFO) undertakes a number of actions. Many of these actions require scientific information including an assessment of habitat requirements, habitat availability, and habitat-related threats to recovery. This scientific advice is developed as part of a Recovery Potential Assessment process.

DESCRIPTION OF AMERICAN EEL HABITAT, BY LIFE STAGE

SPAWNING

Little is conclusively known about habitat required to support the spawning stage of the American Eel. Spawning location is inferred based on the size of leptocephali captured in sampling surveys in the Sargasso Sea (Schmidt 1922; Kleckner and McCleave 1985). The smallest American Eel leptocephali captured were found over a relatively wide area (an approximately 550 km arc) in the southern Sargasso Sea, east of the Bahamas and north of Hispaniola (Haiti and the Dominican Republic; Kleckner and McCleave 1988). While the broad overlap in the spatial distribution of American and European *(A. anguilla*) Eel leptocephali suggests that the two species spawn in close proximity, the smallest leptocephali of the American Eel tend to be found further west than those of the European Eel (Schmidt 1923; McCleave et al. 1987; Monk et al. 2010). There is also temporal overlap in spawning of the two species, with the American Eel spawning season taking place primarily from February to April (peaking in March) and the European Eel spawning season occurring primarily from March to May (peaking in April). The northern limit of American Eel spawning is believed to be defined by distinct temperature fronts, separating surface water masses with high temperature and salinity water to the south and seasonally cooled, lower salinity water to the north (Kleckner and McCleave 1985; Munk et al. 2010). It is thought that high temperature, high salinity waters are required for successful eel spawning (Schmidt 1935). Kleckner et al. (1983) suggest that the American Eel likely spawns in water temperatures between 18 to 19 °C, where salinity can exceed 36 ppt (Kleckner and McCleave 1985). Eggs develop and hatch quickly, within 48 hr, at these temperatures (Oliveira and Hable 2010). The broad distribution of small leptocephali of the American Eel indicates that this species potentially spawns over a larger spawning area than other freshwater eels (Tsukamoto 2006), though the actual zone of spawning is likely quite narrow within a given year. It is estimated that the Atlantic eels (American and European) spawn over an east-west oriented spawning zone that is at least 2,200 km long (Tesch 2003).

There remains some debate over whether Atlantic eels spawn over more structurally complex sea mounts or in greater depths of apparently featureless bottom in the open ocean (Fricke and Tsukamoto 1998; McCleave 2003). Despite concerns that eels that migrate individually would be unable to find mates in the open ocean (Fricke and Tsukamoto 1998), there is general consensus that the smallest leptocephali (Kleckner and McCleave 1985; Castonguay and McCleave 1987) are captured far enough away from sea mounts that they likely could not have dispersed from those habitat features (Tesch 2003). It is likely that Atlantic eels spawn in the upper 300 m of the water column, based on temperature and salinity gradients and the presence of pre-leptocephali with oil globules at those depths, indicating that bottom substrate is not important for spawning eels (Tesch 2003; Greene et al. 2009). Typical water depths in the spawning area are about 6000 m.

LARVAE (LEPTOCEPHALI)

All recruitment of American Eel leptocephali to Canadian waters from the Sargasso Sea occurs via the Gulf Stream. While the oceanography of the Sargasso Sea is poorly understood making it difficult to entirely understand larval transport mechanisms, the initial movement of American Eel leptocephali from the spawning ground is likely from passive drift in the Antilles Current, a seasonal current that flows northwesterly towards the more consistent Florida and Gulf Stream currents (Figure 2; Kleckner and McCleave 1985; Miller et al. 2009). This transport occurs in the upper 350 m of water (Kleckner and McCleave 1985; Tesch 2003; Munk et al. 2010). Not all leptocephali are transported in this current however, as smaller numbers of leptocephali are transported in almost every direction (Kleckner and McCleave 1985). Leptocephali less than 5 mm long were captured at depths between 50 and 350 m by Castonguay and McCleave (1987). Once larger than 5 mm, leptocephali appeared to vertically migrate, as they were observed in shallower (50-100 m) depths at night and deeper (250-300 m depths) during the day (Castonguay and McCleave 1987).

The Florida Current presumably transports the majority of leptocephali northward to the Gulf Stream, which continues to transport leptocephali northward along eastern North America (Miller et al. 2009). By August, leptocephali are ~40-60 mm and are broadly scattered along the western Atlantic Ocean over many thousands of kilometres (Figure 3; Kleckner and McCleave 1985; Tesch 2003). It is believed that the vast majority of American eels metamorphose into glass eels in their first year (Kleckner and McCleave 1985). An active transport mechanism is thought to be necessary for leptocephali and glass eels to exit the Gulf Stream and transit continental shelf slopes and shelves (Kleckner and McCleave 1985), particularly as European Eel larvae are not found exiting the Gulf Stream at this point. Substrate is not thought to be important for this life stage, as leptocephali are found at a range of depths and can tolerate a wide range of temperatures and salinities (Greene et al. 2009).

GLASS EEL / ELVER

Marine

Most American Eel leptocephali metamorphose into glass eels in the ocean over an area spanning many thousands of kilometres (Figure 4; Kleckner and McCleave 1985). Although very little is known about metamorphosis, it is presumed to occur primarily outside of the continental shelf (Tesch 2003). Ingress to nearshore areas is thought to involve active swimming and selective tidal transport and is estimated to take at least 60 days (Wuenschel and Able 2008). Ingress occurs later with increasing latitude (Vélez-Espino and Koops 2010). Glass eels have been sampled over all water depths on the Scotian Shelf (Bradford 2013). In the Gulf of St. Lawrence, glass eels migrate slowly (10-15 km/day) at night (Dutil et al. 2009). The majority of the glass eels in these surveys were captured in May and early June (Dutil et al. 2009). Substrate is once again not thought to be important for this life stage, and glass eels can tolerate a wide range of temperatures and salinities (Greene et al. 2009). Once glass eels begin feeding they become increasingly pigmented and are called elvers.

While many American eels migrate into freshwater, some end their migration in nearshore coastal waters and estuaries and complete their yellow eel phase without ever accessing freshwater (e.g., Morrison et al. 2003; Lamson et al. 2006). The decision to migrate or remain in marine or estuarine habitats is influenced by the physiological and hormonal condition of the elver; poorer condition individuals are more likely to cease migration and reside in marine or estuarine habitats (Edeline et al. 2005, 2006; McCleave and Edeline 2009).

Estuarine

Once in nearshore coastal areas, American and European glass eels enter estuaries by drifting at night (Dutil et al. 1989) on flood tides, and burrowing into or using protective substrates to hold position during ebb tides (Deelder 1952; Creutzberg 1961; Kleckner and McCleave 1982; Wippelhauser and McCleave 1987). The importance of diurnal movements appears to diminish as the season progresses, and elvers become more active during the day at this point (R. Bradford, DFO, personal communication). There are portions of the tidal/lunar phases during the late (near-shore) stages of the continental migration that are important for glass eel recruitment, and Tesch (2003) used the knowledge of the influence of tidal currents and negative phototactic responses to postulate a 14 day rhythm of activity to predict glass eel ingress. The use of the sea bottom as shelter during ebb tides may be important for successful migration at this stage (Greene et al. 2009).

Freshwater

Across their range, glass eels enter freshwater beginning in late winter. In Canada, they enter rivers between late April and early August, with the peak of ingress occurring earlier in rivers closer to the spawning area (Jessop 1998; Dutil et al. 2009). Environmental predictors of glass eel runs are variable, but increased temperature and reduced flow (corresponding to lower water velocity) in rivers early in the upstream migration season may trigger upstream movement (Martin 1995; Jessop 2003). Throughout the migratory period glass eels typically enter freshwater at night at flood tide, mostly during spring tides (rather than neap tides). Glass eels are believed to be attracted to freshwater via chemosensory cues (Creutzberg 1961; Sorenson 1986).

Eels begin moving upstream when stream water temperatures reach 10°C and continue until temperatures exceed 20°C, with peak migration occurring at temperatures between these extremes (Helfman et al. 1984; Sorensen and Bianchini 1986; Haro and Krueger 1988; Jessop 2003). Water temperatures lower than 10°C can result in a pause in migratory behaviour until temperatures increase again (Jessop 2003). After stimulating migration into freshwater, temperature and water flow do not seem important to eel movement. While glass eels in estuaries are initially active primarily at night, once in freshwater elvers are increasingly active during the day (Sorensen and Bianchini 1986).

Elvers that enter freshwater may spend much of this life stage migrating upstream (Haro and Krueger 1991). Using an experimental flume, Barbin and Krueger (1994) found that elvers moved upstream in water velocities ranging from 10-40 cm/s using burst-swimming through the hydraulic boundary layer and water column, between periods of rest in the substrate. At higher water velocities, elvers spent more time resting between movements. In velocities exceeding 35 to 40 cm/s, elvers had difficulty swimming and maintaining their position (Barbin and Krueger 1994). Jessop (2000) also noted that eels sought the protection of substrate at water velocities greater than 25 cm/s. Barbin and Krueger (1994) calculated that elvers could move upstream 100 m/day at a water velocity of 30 cm/s. Evidence from field studies contrast this finding, as average movements of 6 and 15 m/day were estimated by Haro and Krueger (1991) and Jessop (2000) under similar flow conditions. American eel elvers took 1 month to move ~180 m upstream (Haro and Krueger 1988), which may be a result of time required to physiologically adapt to freshwater (Sorensen and Bianchini 1986). However, there are also anecdotal reports of elvers moving quickly large distances upstream, including a 120 km upstream migration in the St. John River over only a couple of weeks (R. Bradford, DFO, personal communication).

Analysis of stomach contents of elvers from the Petite Trinité River on the north shore of the Gulf of St Lawrence indicated that elvers fed mainly on insect larvae (Dutil et al. 1989). Jessop (2000) suggested that a major source of predation on American Eel elvers in the East River, Nova Scotia, was cannibalism by larger conspecifics. Jessop (2000) cites Barker (1997), who identified about 4% of the total diet of yellow eels as elvers.

YELLOW EEL

Recent understanding of yellow eel habitat shifts across salinity boundaries has primarily come from microchemistry studies, in which otolith Sr/Ca ratios are used to indicate the habitat of residency over lifetime profiles. Yellow-phase American eels display a variety of migration patterns, with some eels migrating into, and residing in, freshwater until maturity, with others remaining in estuaries and nearshore coastal areas and never entering freshwater, while a third pattern has eels migrating back and forth between freshwater and marine habitats (Morrison et al. 2003; Lamson et al. 2006; Thibault et al. 2007a; Jessop et al. 2008). The frequency of inter-salinity movements varies with distance from the sea; such movements are common among eels in freshwater that are close to saline waters, but rare or absent among eels in freshwater that is distant from the sea (Lamson et al. 2006).

Reported movements between fresh and saline water are typically irregular in nature, with interhabitat shifts occurring once to several times during the animal’s lifetime (Jessop et al. 2008). A second type of interhabitat movement is seasonal, with eels moving between summer feeding grounds and winter dormancy grounds. However, Thibault et al. (2007b) and Jessop et al. (2008) presented evidence that suggested that the otolith Sr/Ca method may underreport movements to a seasonal wintering ground because of low winter otolith accretion due to low winter metabolism. Recent research has confirmed that otolith microchemistry fails to detect eel movements to freshwater wintering grounds in coastal streams and estuaries in Fundy National Park, New Brunswick (D. Cairns, DFO, personal communication). The research also found that stable isotope analysis was likewise unable to detect such movements. These findings suggest that seasonal movements between fresh and salt water may be more common than previously appreciated. Migrations between estuarine summering grounds and fresh wintering grounds might be due to higher overwinter survival in fresh water and greater food availability in estuaries (Thibault et al. 2007b). However, there is no clear evidence either that freshwater offers superior wintering survival, or that food is more available in estuaries.

Regardless of the habitat mode, eels may remain in the yellow phase for over 20 years before maturing and outmigrating (reviews by Helfman et al. 1984; Tesch 2003; Jessop 2010). In large river systems such as the St. Lawrence River, the upstream migration of yellow eels is seasonal (summer) and protracted as it may last several years before eels settle in an area where most of the growth phase will take place (Castonguay et al. 1994).

Marine

Little is known about the habitat of yellow eel in the oceanic environment, but there are reports of yellow eels being captured in Canadian waters in the months of May, June and July which would suggest that these are not spawning phase individuals (Bradford 2013). These captures occurred over a wide depth range, including locations > 100 m in depth (Bradford 2013).

Estuarine

American eels are widespread and often common in sheltered bays and estuaries off the east coast of North America. In the North Sea, open marine waters were a major habitat for yellow European eels, and supported fisheries whose annual harvests peaked at >300 t (ICES 2009). In contrast, yellow American eels rarely occupy open marine waters. Beyond these broad generalizations, it has proven difficult to define patterns of American Eel habitat use that are consistent across all saline waters.

Cairns et al. (2012, 2014) mapped waters off the east coast of North America according to the degree of exposure to the open sea. In eastern Canada most (93.8%) recorded eel fishing locations were within the sheltered category, which was defined as waters inside a line drawn between the points where a 1.5 km diameter circle first touch the sides of an inlet. This suggests that sheltered habitat as defined by this scheme can be taken as a first approximation of yellow eel habitat in saline waters. However, fishing distributions do not necessarily encompass all occupied habitat. Notably, fishers could avoid more exposed waters in order to reduce the risk of gear damage in storms.

To further explore the distribution of eels in saline waters, Poirier (2013) analyzed data from 25 trawl, beach seine, and long-line surveys on the east coast of North America. Results of surveys in open marine waters supported earlier suppositions that such habitat is rarely used by American eels, except possibly in a narrow fringe along the coast. Catch rates of eels in coastal waters varied substantially among surveys, which may reflect, at least in part, variations in gear efficiency for eel capture. In most surveys that had substantial eel catches, eels were commonly taken in sheltered waters, but they were also taken in semi-exposed waters (defined as waters between the sheltered zone and lines drawn between the points in a 15 km diameter circle contacting the sides of an inlet) in some surveys. Survey results indicated that eels were common in estuaries in Chesapeake Bay that are too wide to be classed as sheltered, and also in a fringe along the coast of Delaware Bay. Consequently, Cairns et al. (2014) proposed that saline-water yellow eel habitat on the east coast of North America can be approximated as sheltered habitat, plus the Delaware Bay and Chesapeake Bay habitat as noted above.

Figures 5 to 7 show eel depth-abundance relations from the surveys as summarized by Cairns et al. (2014), and also from a literature compilation by Cairns et al. (2012). At each location, there is typically a distinct depth-abundance pattern, ranging from decreased abundance with depth to increased abundance with depth. However, there is no consistent depth-abundance relation across study locations. In some cases eels are present, and may reach peak abundance at depths >25 m. The large commercial trawl fishery for European eels in the North Sea operated mainly at depths between 10 and 50 m (ICES 2009).

Hallett (2013) surveyed American eels in southern Gulf of St. Lawrence bays, estuaries, and fresh-water ponds at night from a light-equipped glass bottom boat. Eels were always close to the substrate, or (rarely) associated with vegetation floating in the water column. Eel abundance did not vary with vegetation density, within the range of vegetation cover which allowed eels to be seen.

Eels kept in captivity by Tomie (2012) preferred to conceal themselves in mud bottom over cobble bottom, and shunned sand and gravel bottoms. Eels can readily burrow in mud and can easily enter interstitial spaces in cobble, which likely explains their preference for these substrates.

Yellow eels in northeastern North America, but not further south, show much faster growth in saline than in fresh water (Cairns et al. 2009, 2014). In eels, maturity is size-dependent, with eels becoming silver when they reach a certain size that is specific to the geographic area. The use of both fresh and saline waters in northeastern North America has been termed a paradox because the extended time to maturity in freshwater should increase cumulative mortality, and decrease lifetime fitness, in fresh water habitats, provided that annual natural mortality does not vary with habitat (Cairns et al. 2009). Mean eel densities did not vary across salinity boundaries in PEI watercourses and in the tidal Hudson River estuary (Cairns et al. 2009). In contrast, within a tidal Delaware Bay estuary, eel CPUE increased with increasing salinity (Cairns 2009). In estuaries that are tributary to Chesapeake Bay, the proportion of sets that caught eels tended to increase near and above the limit of salt penetration (Cairns et al. 2014)

Eels viewed at night from a glass bottom boat in southern Gulf of St. Lawrence bays, estuaries, and freshwater ponds have an approximate lower size limit of 350 mm (Hallett 2013). This is not an artifact of the method, because water clarity was such that smaller objects were readily seen on most survey nights. Ungraded catches in fyke net fisheries in the same areas have similar size distributions. This raises the question of the whereabouts of eels smaller than 35 cm, though eels smaller than this size are regularly captured in Bras D'or Lake in Cape Breton (S. Denny, Unama'ki Institute of Natural Resources, personal communication). In Sweden, biologists using mud dredges have located substantial numbers of small eels in shallow vegetated bottoms (ICES 2009). It is possible that eels <350 mm live furtively in vegetated areas to reduce cannibalism risk from larger conspecifics.

American eels exhibit temperature-dependent winter dormancy. Captive eels held in tanks at ambient temperature consistently remained in winter burrows at temperatures below about 4^{o}C, and left them in the spring at about the same temperature (Tomie 2012). Some eels leave summer estuary habitat to winter in freshwater (Thibault et al. 2007b; Jessop et al. 2009). However substantial numbers of eels winter in the mud of bays and estuaries of the southern Gulf of St. Lawrence (Cairns et al. 2012; Tomie 2012). Assays of body fluids of eels sampled in winter from this habitat failed to reveal anti-freeze activity. Nevertheless, these eels are able to stay in mud below waters that are $<0^{o}$C, possibly because temperatures of seafloor mud are warmer than those of the overlying water (Tomie 2012).

Eels that bury in mud breathe brachially either by positioning their mouths just at the substrate surface, or by maintaining a breathing shaft between the mouth and the substrate surface (Tomie 2012). No evidence was found for cutaneous breathing. Given their breathing method, eels can respire successfully regardless of the oxygen concentration within the substrate.

A portion of American eels from St-Jean River (near Gaspé, Québec) exploit the brackish estuary as a summer feeding area (Thibault et al. 2007). At least some of these eels return to the river to overwinter. This study also revealed that American eels in the estuary were active at night but homed to specific daytime resting sites.

Freshwater

Yellow eels are found in both lotic and lentic waters in freshwater, from the high-water mark to at least 15 m in depth (MacGregor et al. 2010). Eels were captured at all trawl depths (1-33 m, mix of freshwater and saline sites) sampled by Geer (2003) in Chesapeake Bay, though the majority of eels in that study were captured between 4 and 10 m. Yellow eels are primarily benthic, and use substrate (rock, sand, mud), and bottom debris such as woody debris and submerged vegetation for protection and cover. They appear to be habitat generalists, with little consistent preference for habitat type, cover, substrate, or water temperature (Wiley et al. 2004). In Maryland, Wiley et al. (2004) observed a weak relationship between eel density and diversity of water depths/velocities, and smaller eels were also associated with faster currents and larger eels with slow, deep habitats (Meffe and Sheldon 1988). In New York, Machut et al. (2007) found smaller eels associated with cobble and gravel, and larger eels associated with larger cobbles, boulders and sand. American eels can also be found in soft sediments (Ford and Mercer 1986; Chaput et al. 1997) and in sediment with aquatic macrophyte growth (LaBar and Facey 1983). In Ontario, smaller stocked eels were associated with gravel and layered bedrock substrates, sites with higher water velocity and sites close to shore. Larger eels were found at sites with boulder substrate further away from dams (Lloyst 2012). Lloyst (2012) argued that while the American Eel fits the definition of a habitat generalist, individuals actually use specific substrate features that change with increasing length; this idea is supported by the fact that the American Eel appears to establish a home range (Dutil et al. 1988; Oliveira 1999; Morrison and Secor 2003). Home ranges reported from freshwater habitats appear larger than those reported from brackish or salt water habitats (Greene et al. 2009). In freshwater, home range area has been estimated to range from 1 ha to 4.7 km (Helfman et al. 1983; Morrison and Secor 2003) and vary with eel size (Thibault et al. 2007a).

American eels are tolerant of a wide range of water temperatures. For example, Geer (2003) captured eels in Chesapeake Bay at temperatures ranging from 3-31°C, with the highest proportion of eels observed from 26-28°C. In the southern Gulf of St. Lawrence, eels winter in mud under waters whose temperatures fall as low as -1.5^{o}C (D. Cairns, DFO, personal communication). In laboratory settings, Barila and Stauffer (1980) identified a preferred temperature of 16.7°C, similar to the 17-20°C preference range found by Haro (1991). Maximum growth in American Eel was observed at 28-29°C (Tzeng et al. 1998). In the closely related European Eel, Nyman (1972) documented a similar optimal summer temperature range for promoting eel swimming and feeding behavior of 13-17°C, with higher temperatures leading to aggressive behaviour. Moreover, optimal growth in the European Eel has been observed in experimental studies at 22-23°C (Sadler 1979). In winter, some eels take refuge in soft substrates and enter torpor in cooler water temperatures. Walsh et al. (1983) held yellow eels at 5°C for over five weeks, and found that at temperatures less than 8°C they stopped feeding and remained inactive for months.

Water temperature is also important for understanding the seasonal movements of American eels. In Nova Scotia, Newfoundland and Québec, eels with ready access to brackish or salt waters may undertake downstream migration in spring from freshwater to forage in the salt water environment and migrate back to freshwater for overwintering (Medcof 1969; Jessop 1987; Jessop et al. 2006; 2009; Thibault et al. 2007a). In the York River on the Gaspé Peninsula, Québec, 50% of eels trapped and released in the river moved into the estuary for the summer (Hedger et al. 2010). On Prince Edward Island, Cairns et al. (2004) did not find seasonal movements between freshwater and estuarine water and speculated that the head-of tide impoundment may restrict seasonal movements. These movements between fresh and saline waters are thought to facilitate faster growth, as saline waters are associated with higher growth rates (Helfman et al. 1987; Lamson et al. 2009). In Ontario (Bonnechere River), American Eel have been observed moving downstream in the fall from hard clay bottoms to areas in the lower reaches with mud or silt bottoms (MacGregor et al. 2010). The onset of upstream migration in yellow eels is also triggered by increasing water temperature. In a Rhode Island stream, yellow eels moved upstream when water temperatures were between 10-20°C (Haro and Krueger 1991). In the St. Lawrence River, the daily capture of yellow eels ascending eel ladders peaked when water temperatures reached 22-23°C (Verdon and Desrochers 2003). Most eel activity, including upstream movement, occurs predominantly at night (Verdon et al. 2003; McGrath et al. 2003a; Hedger et al. 2010) and movement through eel ladders may be disrupted by artificial light (Verdon et al. 2003).

Upstream movement may be impeded or obstructed by large vertical barriers. To traverse obstructions, eels may need to exit the water and crawl on wet and rough surfaces (Tremblay et al. 2011). Eels of all sizes can climb slopes with surface irregularities or vegetation; American eels have been observed traversing damp substrates such as moss, grass, rocks and cement (MacGregor et al. 2010; COSEWIC 2012). However, only small eels (<10 cm) can ascend vertical or near vertical barriers (Legault 1988).

Barriers that restrict or impede upstream movement may lead to a concentration of eels immediately downstream of the barrier (Wiley et al. 2004; Machut et al. 2007; Lloyst 2012). It is speculated that the high density of eels in these regions may increase cannibalism, predation, competition for food, or disease, and negatively affect eel growth (Haro et al. 2000; Wiley et al. 2004; Stacey 2013). In New York, eels that had to deal with obstructions at densities of < 0.5 barriers/km had significantly better condition than eels that had to circumvent obstructions at densities of more than 0.5 barriers/km (Wiley et al. 2004).

The American Eel inhabits both lotic and lentic waters, hence it can tolerate a wide range of flow conditions. Most studies have found flow to be of little or no predictive value for eel occurrence, though size-specific habitat preferences were noted with larger eels preferring slow, deep habitats and smaller eels preferring faster currents in one study (Meffe and Sheldon 1988), and the presence of a variety of velocity-depth habitats were important for modeling eel presence in Maryland rivers (Wiley et al. 2004). Upstream movement may also be impeded or obstructed by high velocity currents, though flow velocities that restrict movement are poorly understood. During upstream migration, movement tends to occur during periods of low flow velocity, typically midsummer. Legault (1988) identified 0.5m/s as the upper laminar flow velocity for the European Eel. Knights and White (1998) report that European eels < 100 mm are able to swim against currents of 1.5-2.0 m/s and Solomon and Beach (2004) describe burst speeds in European eels in the 400-600 mm length range as 1.25-1.35 m/s.

The distribution of American eels may be limited by low dissolved oxygen levels (Rulifson et al. 2004; Greene et al. 2009). In North Carolina, abundant catches of American eels were nearly always in waters with dissolved oxygen levels above 4 mg/L (Rulifson et al. 2004). Less than 2% (122 of 7182) of the eels captured by Geer (2003) were at sites with dissolved oxygen levels < 4 mg/L.

American eels feed on a wide variety of prey items including fish, molluscs, crustaceans, insect larvae, surface dwelling insects, worms, and plants (e.g., Ogden 1970; Facey and LaBar 1981; Lookabaugh and Angermeier 1992; Denoncourt and Stauffer 1993; Stacey 2013). Food type varies with body size, with smaller eels (< 40 cm total length) ingesting a wide variety of aquatic insect orders, and larger eels ingesting mostly fish and crayfish (Lookabaugh and Angermeier 1992; Stacey 2013). It is believed that American eels feed primarily at night (Sorenson et al. 1986).

SILVER EEL

Yellow eels transform into silver eels before returning to the open ocean for their migration to the spawning area in the Sargasso Sea. Transformation involves gradual changes that result in fully mature spawning adults, including a change in color to a bronze black sheen, fattening of the body, thickening of the skin, enlarged eyes, and degeneration of the digestive tract (reviewed by Facey and Van den Avyle 1987).

Freshwater

Peak outmigration from freshwaters typically occurs in pulses in the fall, with downstream migration believed to be initiated by environmental factors such as water temperature, river or stream discharge, water level and/or precipitation events, and light intensity, including moon phase (e.g., Haro 1991; Richkus and Dixon 2003). Downstream migration occurs predominantly at night (or in darkness) and is frequently associated with heavy precipitation and high-flow events (see review by Richkus and Dixon 2003). No detailed studies have been made on downstream swimming behaviour of American eels in the wild. However, experimental studies on the European Eel indicate that passive drift, controlled drift and active downstream movement were all used (Richkus and Dixon 2003). Downstream migrations occur in bursts with long periods of no movement and peaks of intensive movements. It is possible that continued downstream migration may require repeated specific environmental cues (Richkus and Dixon 2003).

Downstream migration by silver eels in the St Lawrence River watershed may be initiated by different triggers than elsewhere. In the freshwater portion of the St Lawrence River, migration from Lake Ontario and Lake Champlain may begin as early as May, peaks in summer (July-September), and appears unrelated to environmental conditions (McGrath et al. 2003b). In mid-summer, water temperatures are highest (often exceeding 20°C) and flow rate is low (MacGregor et al. 2010).

Analysis of catch-per-unit effort data from near Québec City in the St Lawrence River suggests that the median eel capture date in summer was earlier in years with high water level (and flow) and later in years with low water level (and flow) (de LaFontaine et al. 2009). Hydrological and climatic conditions in August/September strongly affect migration activity and the distribution of eels in the lower part of the river. Mean water level (and flow) has dropped in the St Lawrence River since the 1970’s, and corresponds with later median capture dates of eels in the Lower St Lawrence River. de LaFontaine et al. (2009) speculate that delayed seaward movement may subsequently affect gonadal development, arrival of eels at the breeding grounds, time of spawning and larval hatching success in the ocean.

There is little evidence that substrate or depth are important habitat features for outmigrating silver eels (Greene et al. 2009). In the St. Lawrence River, outmigrating silver eels were primarily captured in 4-10 m depths, with low catches nearer the surface (McGrath et al. 2003b).

Estuarine

Outmigration from estuaries occurs over a narrower timeframe than freshwater, with migration occurring in the fall (late September or October) in short bursts primarily at night (Barbin et al. 1998; Verreault et al. 2003). Migration from the St Lawrence River estuary to the ocean occurs over a short period (approximately 1 month, primarily October) in the fall (Caron et al. 2003; McGrath et al. 2003b; Verreault et al. 2003). The time between peak migration through the St Lawrence River and movement from the estuary suggests that silver eels may be staging prior to movement from freshwater to saltwater, however no concentration of eels suggesting a staging area has been found (McGrath et al. 2003b). American eels at the silver eel stage in the St. Lawrence estuary do not complete the downstream migration in one continuous direct movement, with eels pausing at various locations (Béguer-Pon et al. submitted). High individual variability in migratory longitudinal profiles and speed was documented with no apparent relation to river discharge or morphological traits. Migration speed increased over the season in concert with decreasing day length. Speed decreased as the eels moved downstream. Moreover migrating silver eels in the St. Lawrence are largely nocturnal and use selective tidal stream transport to leave the estuary.

Barbin et al. (1998) found American eels In Maine outmigrating in September and Octoberin water temperatures ranging from 9.6°C to 17.6°C. In a laboratory study, Haro (1991) found silver eels preferred a water temperature of 17°C.

One recent acoustic tracking study through a southwestern New Brunswick macro-tidal estuary and bay indicated that silver eels initiated their seaward migrations around or shortly after sunset, mostly migrated at night, exhibited no bias for migration on ebb versus flood tides, and swam both with and against tidal currents with little preference for depth (Bradford et al. 2009). Silver eels were estimated to maintain a relatively constant horizontal swimming speed equivalent to about 0.5 body lengths per second (Bradford et al. 2009). However, transit times and distances were sensitive to tidal phase (i.e., the direction of the tidal current relative to the direction of transit of the eels) and tidal current speed (Bradford et al. 2009). The results of this study are in contrast to those of Parker and McCleave (1997) who found that silver eels used selective tidal stream transport during outmigration from an estuary, using the substrate to rest during flood tides and rising near the surface during ebb tides.

Marine

Once back in the open ocean, it appears that silver eels remain relatively near the surface. Wenner (1973) reported spawning-phase American Eel captures from nearshore coastal areas in November and December in depths ranging from 9 to 82 m and water temperatures from 8-12°C. Silver American eels equipped with satellite tags in the Gulf of St. Lawrence performed diel vertical migrations from approximately 30 m at night to 200-250 m during the day with ambient temperatures fluctuating from 9°C at night to 3°C during the day (Béguer-Pon et al. 2012). These temperatures are only for the northern part of their range; as eels migrate further south, the water temperatures that they experience will increase. European eels in the ocean also undergo diel vertical migrations, swimming in the upper 250 m of water in the evening, and diving down to depths deeper than 500 m during daylight hours (Tesch 1978; Aarestrup et al. 2009). The observed depth range and behavioural pattern fit the physiological changes in silver eels, including the color change and changes to the visual system which would aid in predator avoidance at these depths, and morphological changes to the swim bladder which would aid in the diel vertical migration (McCleave and Kleckner 1985). There was little temperature difference between the depths occupied during the day (mean ~10.1°C) and night (mean ~11.7°C; Aarestrup et al. 2009). These depths are also consistent with a calculated physiological limit of descent for the European eel of some 600 m (Tesch 1995).

A summary of features, functions and attributes of habitat required for the American Eel can be found in Table 1.

ESTIMATES OF THE AMOUNT OF HABITAT OF VARIOUS QUALITIES / PROPERTIES PRESENT FOR EEL

Historically, the American Eel used all rivers and tributaries accessible from the Atlantic Ocean from Venezuela in the south through the Gulf of Mexico to mid-Labrador in the north. In the United States they occurred as far inland as the Mississippi River, and in Canada, inland as far as Niagara Falls and the headwaters of the Ottawa River (Figure 8; MacGregor et al. 2010).

Likely because of this broad distribution, few attempts have been made to quantify the amount of habitat available for the American Eel. The extent of occurrence (defined as the area contained within the shortest continuous imaginary boundary which can be drawn to the present occurrence of a taxon) and biological area of occupancy (defined as the area occupied by a taxon) in Canada were estimated to be 2,065,932 km^2 and 1,652,200 km^2, respectively (COSEWIC 2012).

MARINE

The marine waters of the Atlantic Ocean support the spawning, egg and larval stages of the American Eel. Spawning takes place in the Sargasso Sea in and south of thermal fronts that separate the northern from the southern Sargasso Sea from approximately 19.2°N to 29°N and 52°W to 79°W (Kleckner and McCleave 1985; Tesch 2003). The width of this area is estimated to be between 550 km for the American Eel (Kleckner and McCleave 1985) and 2200-2500 km for both the American and European eels (Tesch 2003), resulting in an area of potential spawning habitat encompassing several thousand square kilometers (COSEWIC 2012). Leptocephali and glass eels occupy the most extensive range (over 10,000 km) of continental shelf waters of any fish in the Americas, ranging from 7°N to 55°N (Helfman et al. 1987; MacGregor et al. 2010).

Semi-exposed, exposed bay, and exposed ocean habitat included 22,640, 261,928, and 618,302 km^2 off the east coast of Canada, and 20,681, 15,881, and 377,091 km^2 off the east coast of the US, respectively (Cairns et al. 2014). This classification scheme extends to the 500 m depth contour. This habitat would be used by leptocephalli and glass eels on their migration to the coast and by silver eels on their return migration to the spawning grounds. Some semi-exposed habitat is also used by yellow eels.

ESTUARINE

Based on the exposure classification system of Cairns et al. (2012) and the distribution of eels reported in marine surveys, Cairns et al. (2014) considered that saline yellow eel habitat on the east coast of North America included 8,910 km^2 in Canada (including Saint-Pierre and Miquelon) and 14,360 km^2 in the US for a total of 23,279 km^2 for eastern North America. Sheltered habitat constitutes only 1.1% of marine habitat out to the 500 m contour off eastern Canada, yet it contains 93.8% of the eel fisheries (Cairns et al. 2012).

FRESHWATER

Ontario

The American Eel was historically found in all accessible tributaries of Lake Ontario and the St Lawrence and Ottawa River systems, but are currently found in only a portion of this range (Figure 9; MacGregor et al. 2010). In the Canadian portion of the Lake Ontario and St Lawrence River systems, Verreault et al. (2004) estimated that there are 8,411 barriers of at least 2.5 m in height that prevent, restrict or delay access to 12,140 km² of potentially suitable habitat for American Eel. Similarly, MacGregor et al. (2010) identified 953 dams within the eel’s historical range in Ontario, including 87 hydroelectric facilities within the historic range of eels (Figure 10). COSEWIC (2012) provided an estimate of available habitat of 97,400 km² in National Freshwater Biogeographic Zone 10, which encompasses all freshwater habitat in the St. Lawrence River watershed up to the influence of tidal waters in the St. Lawrence River near Québec, including all Ontario waters (Table 2). In the Canadian portion of the Lake Ontario and St Lawrence River systems, it is estimated that 87% of this historic area is still available to

American Eel, with 8,411 barriers of at least 2.5 m in height that prevent, restrict or delay access to 12,140 km² of potentially suitable American Eel habitat.

Ottawa River watershed

Eels once ranged as far north as Lake Timiskaming and its tributaries, such as the Blanche River, and Lake Nipissing. However, eels are now believed extirpated from all tributaries of the Ottawa River above Des Joachim Hydroelectric facility at Ralphton (fourth barrier on the Ottawa River from the confluence at the St Lawrence River) and above the Renfrew Power Generation facility at Renfrew on the Bonnechere River. They were recorded from the Petawawa River near the Boundary of Algonquin Park in 2002 (MacGregor et al. 2010). Eels are still found in the lower reaches of the Ottawa River at low densities, and in the lower reaches of the Mississippi River subwatershed. MacGregor et al. (2010) noted that none of the barriers on the Ottawa River system have facilitated upstream or downstream eel passage, and Verreault et al. (2004) estimated that 3,700 km² of suitable eel habitat were lost above barriers in these watersheds.

St Lawrence River and Lake Ontario watershed

Tributaries of the St Lawrence River and Lake Ontario such as the Gananoque, Cataraqui, Napanee, Salmon, Moira, and the Trent-Otonobee once supported abundant eel numbers. Now, only small numbers of eels may persist in the lower reaches of tributaries of Lake Ontario, particularly the Trent, Moira, Salmon, Napanee and Cataraqui Rivers. Eels were once abundant along the Lake Ontario shoreline near to and within the lower Niagara River (below the falls), and were found in many inland watersheds of the Niagara Peninsula. Verreault et al. (2004) estimated that 5,800 km² of suitable eel habitat were lost above barriers in this watershed.

There are two main hydroelectric generating station complexes on the St Lawrence River below Lake Ontario; the Moses-Saunders and Beauharnois (located in Québec – see below) generating stations. Upstream movement at the Moses-Saunders Dam is provided by two permanent eel ladders (one on the Canadian side established in 1974 and one on the New York side established in 2006) and by the shipping locks. McGrath et al. (2003a) estimated that only 23% of eels attempting to ascend the Canadian ladder were successful, though improvements to the ladder (different substrate, building of an extension pipe at the top of the dam) have greatly improved passage efficiency (R. Threader, Ontario Power Generation, personal communication). Upstream passage is not provided at any other barrier, and downstream passage is not provided at any hydroelectric facility in the watershed.

Québec

The American Eel was historically found in all accessible tributaries of the Gulf of St Lawrence and the St Lawrence River. No detailed assessment of the current distribution of American Eel could be found in the literature. COSEWIC (2012) provided an estimate of available habitat in National Freshwater Biogeographic Zones 10 (97,400 km²) and 11 (161,400 km²; Table 2). Zone 10 encompasses all freshwaters in the St. Lawrence River watershed up to the influence of tidal waters in the St. Lawrence River near Québec and is shared with Ontario; zone 11 includes both freshwater and marine habitat in the lower St. Lawrence River, the north shore of Gaspe, and the north shore of the Gulf of St. Lawrence (Table 2). Verreault et al. (2004) estimated that 1,200 km² of suitable eel habitat were lost above barriers in one portion of National Freshwater Biogeographic Zones 10 in Québec, the Richelieu River-Lake Champlain watershed, and an additional 1,440 km² were estimated to have been lost in Québec in other watersheds within the St. Lawrence River watershed (Verreault et al. 2004).

The Centre d’Expertise Hydrique du Québec (CEHQ) database identified 4,994 dams in the St. Lawrence watershed and an additional 137 dams in the Rivière Saint-Jean watershed (Figure

11; Tremblay et al. 2011). Using this data, Tremblay et al. (2011) calculated preliminary passability ranks for upstream and downstream movement through each dam, using a passability index loosely based on Steinbach (2006). They noted that the CEHQ database was not designed to calculate passability ranks for fish, and so important variables were often absent or were infrequently recorded. The ranks were not validated using field assessments of each dam or using measures of eel abundance below or above each dam. Two variables were used to describe upstream movement passability: dam height and dam material type. Using these variables, one dam was passable without apparent difficulty, 5.5% were partially passable, 5.3% were nearly impassable and 86% were impassable (Tremblay et al. 2011). Validation of these results using aerial photograph interpretation of the dams supported the identification of impassable dams, but suggested that classification of the other passability ranks was less reliable because no assessment of slope was available in the CEHQ database. For downstream movement, passability was described using two variables: the presence or absence of a hydroelectric dam, and dam height. Using these variables, 86% of dams caused significant delays (partially passable), 9.6% caused significant delays and mortality (nearly impassable), and 4.9% were impassable (100% mortality; Tremblay et al. 2011). Tremblay et al. (2011) did not calculate the amount of habitat that these obstacles prevent, restrict or delay access to.

At the first main barrier in the St. Lawrence River, the Beauharnois generating station located near Montreal, a manual capture-release passage facility has operated since 1994, with the exception of 1996 and 1997 when it was not functional, and shipping locks are also present. In 2002 an eel ladder was opened on the west side of the dam and in 2004 another eel ladder opened on the east side of the dam (Bernard and Desrochers 2007). A sharp decline in silver eel catches in the Richelieu River in the Lake Champlain watershed, along with a significant increase in eel size was attributed, in part, to the reconstruction of barriers at Chambly and Saint-Ours in the 1960’s; eel ladders were constructed at Chambly in 1997 and at Saint-Ours in 2001 (Verdon et al. 2003). Verdon et al. (2003) estimated that 57.4% of the eels that ascended the eel ladder at the Chambly Dam successfully passed the barrier.

New Brunswick

No detailed assessment of the current distribution of American Eel in New Brunswick could be found in the literature. However, eels are frequently captured during fish assemblage surveys in numerous streams, lakes, and estuaries indicates that they occur in all accessible tributaries of the Bay of Fundy and Gulf of St Lawrence (Cairns et al. 2008; R.G. Bradford, DFO, unpublished data). Furthermore, recorded occurrences of American eels (Warner 1965) upstream of high natural barriers relative to other diadromous species (e.g., Atlantic salmon (*Salmo salar*; C. Clarke, DFO, personal communication); American shad (*Alosa sapidissima*; Chaput and Bradford 2003) such as Grand Falls on the Saint John River indicate that American eel can be assumed to be naturally widespread in New Brunswick inland waters.

Statistics Canada reports that there are 1,458 km² of freshwater available in New Brunswick. New Brunswick, along with Nova Scotia, Prince Edward Island, and the central and southern parts of Québec's Gaspé Peninsula, are part of National Freshwater Biogeographic Zone 1, which is estimated to contain 635,200 km² of available eel habitat (both freshwater and marine; Table 2).

A complete inventory of man-made barriers to upstream and downstream fish passage in New Brunswick is not available. However, several studies have indicated that dams contributing to habitat loss (impediment to fish passage and/or altering habitat) are probably numerous and wide-spread. Kidd et al. (2011) estimated that there are more than 200 dams within the Saint John River system that impede fish migrations to some extent. Wells (1999) documented barriers on medium and large rivers entering the Bay of Fundy in New Brunswick and discussed the potential of these barriers to impede fish migration. Five (28%) contained no man-made barriers, 6 (33%) contained barriers that apparently permit some fish passage, and 7 (39%) prevent fish passage or block water flow (Wells 1999). Twenty-three percent of these rivers with barriers contained functional fishways or aboiteaux. The specific impact of barriers on eels was not discussed (Wells 1999).

The largest man-made barriers on New Brunswick rivers are those constructed to facilitate the generation of hydroelectricity. There are nine hydroelectric generating facilities licensed to operate in New Brunswick. One is located on the Nepisiguit River which discharges into the southern Gulf of St. Lawrence but it is located at a presumed naturally impassable barrier. The other eight facilities are located on Saint John River[1] (n =6), the St. Croix River[1] (n =1) and the Magaguadavic River, all of which discharge into the Bay of Fundy.

The 55 m high Mactaquac Dam located approximately 28 km above tide-head is the lower-most dam on the Saint John River. Fish passage primarily for Atlantic Salmon, Alewife (*Alosa pseudoharengus*) and Blueback Herring (*A. aestivalis*) is provided by a trap and truck facility (Ruggles and Watt 1975). This facility is not designed for, or suited to, the passage of American eel elvers or juveniles (Jessop and Harvie 2003). However, small numbers of yellow eels may get passed upstream along with alewife and blueback herring (Jessop and Harvie 2003). The recorded bycatch of American eels in juvenile salmonid electrofishing surveys of Saint John River tributaries indicates that since 1992 eels have been widely distributed among the 29,983 km[2] (54%) portion of the river basin lying below the Mactaquac Dam, but virtually absent from the 25,128 km[2] (46%) of the river basin located above the barrier (Table 3).

Nova Scotia

Historically, American eels probably occurred in all accessible tributaries of the Bay of Fundy, the Atlantic Ocean and the southern Gulf of St. Lawrence. No detailed assessment of current distribution could be found in the literature but Cairns et al. (2008) provide eel catch data from electrofishing surveys from a large number of rivers in the Nova Scotia portion of the southern Gulf of St. Lawrence. It is estimated that there are 2,408 km² of freshwater habitat in Nova Scotia (Davis and Browne 1997).

The Nova Scotia Water Control Structure Database (NSWCD) contains records of 586 dams (as of September 2010; Figure 12). As many of these are low-head barriers, it is not thought that they, for the most part, block upstream access for eels (R. Bradford, DFO, personal communication). According to the database, 14% of these dams contained fish passage structures. Fielding (2011) used the Nova Scotia Water Control Structure database to examine habitat loss for salmonids in the Southern Uplands and in the Inner Bay of Fundy in Nova Scotia. In the Southern Uplands, 279 dams blocked access to 3,008 km of stream length, or 9.3% of available habitat, to salmonids. In the Inner Bay of Fundy, 131 dams blocked access to 1,299 km of streams, or 7.1% of available habitat, to salmonids. The extent to which these dams block access to habitat for American eels was not discussed. Wells (1999) also assessed 26 medium and large rivers in Nova Scotia that connect with the Bay of Fundy for man-made barriers, and discussed the potential of each barrier to impede fish migration. Fourteen (54%) contained no man-made barriers, 7 (27%) contained barriers that apparently permit some fish passage, and 5 (19%) prevent fish passage or block water flow. Fifty percent of these rivers with barriers contained functional fishways or aboiteaux (Wells 1999). The specific impact of barriers

---

[1] The Saint John and St. Croix Rivers are international waterways. There are one or more hydroelectric generating stations operating within the U.S.A. portions of these rivers. The lowermost stations on these rivers are licensed to operate by the Province of New Brunswick.

[2] This includes the 8,114 km^2 (15%) of the river basin lying above Grand Falls.

on eels was not discussed. According to COSEWIC (2012), the only monitored eel ladder in the Maritime Provinces was at the Morgan Falls hydro-facility on the LaHave River on the south shore of Nova Scotia. This ladder was operated beginning in 2002 for a few seasons, but was destroyed by a high water event and not rebuilt.

Prince Edward Island

Historically, American Eel probably occurred in all accessible tributaries of Prince Edward Island. No detailed assessment of current distribution could be found in the literature but Cairns et al. (2008) summarizes available data on catches in ponds and estuaries in PEI. While there are many thousands of kilometers of small freshwater streams in Prince Edward Island, there are no large areas of freshwater and Statistics Canada reports that there is no freshwater available in the province.

MacFarlane (1999) stated that there are some 800 dams in Prince Edward Island that may prevent access to stream habitat for salmonid fish, and Guignion (2009) indicated that there are 600 man-made impoundments that may restrict salmonid movement. The extent to which these barriers restrict or prevent movement by American eels has not been described. There are differences in passability among structures though; Lamson et al. (2006) demonstrated, using Sr:Ca otolith microchemistry, that a 2.2 m vertical wooden spillway with earthen dam only permitted upstream movement of elvers and not larger eels, whereas a pond with a 5-chamber pool and weir salmonid fishway facilitated upstream movement of all sizes.

Newfoundland and Labrador

The known geographic range of the American Eel in Labrador extends as far north as the English River and west to the lower Lake Melville region (Veinott and Clarke 2011; Nicholls 2011). Eels are not known to be found above Muskrat Falls on the Churchill River (Nicholls 2011). The American Eel is expected to have historically occurred in all tributaries accessible to the Atlantic Ocean and Gulf of St. Lawrence in Newfoundland. American eels in Newfoundland and Labrador are found in National Freshwater Biogeographic Zones 2 and 8, and the expected areas of eel occupancy in these zones (both freshwater and marine habitat) are 130,700 and 627,500 km^2, respectively (COSEWIC 2012; Table 2).

Little is known about the current freshwater distribution of eels in Newfoundland and Labrador, although major dams associated with hydroelectric power stations near the mouth of major rivers are anticipated to have reduced or prevented access to freshwater habitat (Nicholls 2011). Natural barriers may also limit use of freshwater habitat in Newfoundland, such as on the eastern side of Grand Lake in the Humber River watershed. Nicholls (2011) identified waterways that may be negatively impacted by large dams and hydroelectric generating stations in Newfoundland. In insular Newfoundland, there are 234 barriers associated with hydroelectric stations and 81 barriers associated with municipal water supplies, with 91 of these barriers being >10 m high (Figure 13). In Labrador, one barrier for municipal water supply occurs at Charlottetown (Nicholls 2011). Although Nicholls (2011) described potential habitat affected by hydroelectric dams, further work is required to assess the extent to which each dam provides a barrier to upstream and downstream migration of eels. Many dams are equipped with fishways to allow salmonid passage; however, the extent to which these fishways facilitate eel movement is not known.

United States

Few efforts have been made to quantify availability of habitat to American eels in the United States (Greene et al. 2009), though it is believed that eels have been extirpated from much of the historic range (Figure 14). A study by Busch et al. (1998) found that barriers have greatly reduced the amount of freshwater habitat available to the American Eel. Stream habitat was estimated to be reduced from 556,801 km to 90,755 km, under the assumption that the barriers blocked all migration. Just over 15,000 barriers were estimated to block eel upstream and downstream migration (Busch et al. 1998). This means that only 16% of stream length within the historical range of the American Eel remains unimpeded by dams, with the greatest impairment occurring in the North Atlantic region from Maine to Connecticut (Busch et al. 1998).

In the United States portion of the Lake Ontario watershed Lary and Busch (1997) estimated that there were 455 dams preventing, restricting or delaying access to 24,693 km (or 82%) of potentially suitable habitat.

The US Fish and Wildlife Service's National Wetlands Inventory (NWI) provides a comprehensive classification of all wetted areas in the United States (Cowardin et al. 1979; Dahl et al. 2009). Coverage includes all interior and inshore coastal areas. The classification scheme is hierarchical and includes more than a thousand categories. Cairns et al. (2014) consolidated fresh habitat categories into riverine tidal, riverine nontidal, lacustrine (lakes), and palustrine (marshes and like habitats, and ponds). These are further divided into habitat with and without emergent vegetation. Habitat totals are presented by zones used for habitat modeling in the RPA.

Freshwater habitat without emergent vegetation totaled 3,488 km^2 in the St. Lawrence Basin, 526 km^2 in Scotia-Fundy, 7,067 km^2 in Atlantic Seaboard North, 2,858 km^2 in Atlantic Seaboard Central, and 7,838 km^2 in Atlantic Seaboard South, for a total of 21,777 km^2. Areas given for the St. Lawrence Basin, Scotia-Fundy, and Atlantic Seaboard North include only areas within the US.

The NWI classification includes riverine tidal non-emergent habitat totalling 175 km^2 in Atlantic Seaboard North, 543 km^2 in Atlantic Seaboard Central, and 411 km^2 in Atlantic Seaboard South, for a total of 1,129 km^2 (Cairns et al. 2014). Riverine tidal non-emergent habitat can be considered entirely accessible to eels. NWI provides no breakdown of other habitat by its degree of accessibility to diadromous fishes.

SUPPLY OF SUITABLE HABITAT RELATIVE TO DEMANDS OF EELS AT PRESENT, AND WHEN THE SPECIES REACHES BIOLOGICALLY BASED RECOVERY TARGETS FOR ABUNDANCE AND RANGE

Recovery targets include both distribution and abundance targets, and short-term and long-term objectives. Suitable habitat to meet these targets must be available across the species range. Habitat loss due to barriers restricting access to formerly productive freshwater habitats is apparent, and there are concerns about the quality of habitats available to eels in both marine and freshwater locations across the species distribution.

Habitat quality for eels can be impacted by anthropogenic activities. For example, the ecosystem of Lake Ontario has been greatly altered by the proliferation of exotic fishes and mussels, altering trophic relations and shifting diets and bioaccumulation rates (Mills et al. 2003). It was hypothesized that these changes might alter habitat quality by reducing food availability, physically changing habitat by reducing the availability of interstitial spaces in substrate, and with the resulting increase in water clarity, forcing eels into deeper and thermally less preferred waters (Casselman, 2003; MacGregor et al. 2010). However, these concerns have been somewhat reduced by the high survival, dispersal and rapid growth of stocked eels into these habitats (Pratt and Threader 2011). Similar concerns exist in marine waters with the green crab, which mechanically disturb sediments and have changed trophic pathways (Leonard et al. 1999; Grosholz 2002).

Land-use changes and practices, such as timber harvest, farming and urbanization can affect habitat quality through a reduction in water quality and increased erosion and sedimentation (Machut et al. 2007). For example, Machut et al. (2007) found that American Eel condition significantly decreased as urbanization of the riparian zone increased. Sedimentation leads to infilling of interstitial spaces important to eels as habitat, and may also increase the level of contaminants (MacGregor et al. 2010). There are also concerns in marine waters that physical degradation from trawling has reduced habitat complexity, thereby reducing habitat quality for eels (Thrush and Dayton 2002).

The potential impact of contaminants on American Eel survival, migration success, reproduction, genetic variability and recruitment are not well understood or quantified. However, eels have potentially high exposure risk due to their behaviour of burrowing in sediment, and are particularly sensitive to bioaccumulation of lipophilic contaminants because they are long-lived benthic species with a high fat content (COSEWIC 2012). Eels store lipids during their freshwater phase sufficient to sustain them through spawning migration and gamete maturation. Stored contaminants are therefore mobilized when lipids are catabolized to provide energy for migration, gamete production and spawning (see reviews by Robinet and Feunteun 2002; Geeraerts and Belpaire 2010). Recent investigations into the contaminant burden of American eels in Lake Ontario, where contaminants were historically very high, have concluded that the risk to eel recruitment using available guidelines is currently low (Byer et al. 2013a, b).

HABITAT TO ACHIEVE DISTRIBUTION TARGETS

Habitat access to freshwater in both the United States and Canada has been reduced, perhaps most significantly in association with the construction of large dams having no or inadequate upstream fish passage facilities for American eels (see above). In the United States, only 16% of historic stream length remains completely accessible to eels (Busch et al. 1998). No such assessment has been completed in Canada, though it is apparent that many thousands of kilometers of freshwater habitat are no longer accessible (e.g., Ottawa River, Saint John River). Connectivity among important inland habitats and between inland habitats and estuarine feeding and oceanic spawning grounds is crucial to ensure eels are able to grow, disperse and migrate effectively (MacGregor et al. 2010). In the St. Lawrence River watershed alone, over 14,000 km^2 (13%) of yellow-eel rearing habitat are no longer accessible to eels (Verreault et al. 2004). It is also important to note that the areas of greatest impairment are areas where access to large lakes has been lost, which disproportionally produce large female eels (COSEWIC 2012).

Connectivity among important inland habitats and between inland habitats and estuarine feeding and oceanic spawning grounds is crucial to ensure eels are able to grow, disperse and migrate effectively. It will be impossible to meet any distribution targets that propose to restore access to formerly productive rearing habitats without recognizing that important habitat has been lost due to barriers, and ensuring upstream and downstream passage at strategic barrier locations.

HABITAT TO ACHIEVE ABUNDANCE TARGETS

There are few quantitative estimates of American Eel density available in Canada, and where they exist densities are lower than historical values (Cairns et al. 2014). There is little evidence across the species range for examples of density-dependence, except in a few studies where eels are in high density situations below impassable barriers. Where estimates of available habitat exist (e.g., in marine and estuarine waters, and freshwater in the United States), the amount of habitat available to the American eel is large compared to contemporary eel populations, likely well below the carrying capacity of the habitat, and therefore it is unlikely that production of eels is limited over broad spatial scales at current abundance levels.

It is also clear that habitat access to freshwater areas was lost across the species range and that over the long term, as the eel population grows and recovers, restoring access to these habitats will likely be necessary to achieve long-term abundance objectives.

VARIABILITY IN BIOLOGICAL FUNCTION OF THE HABITAT FEATURES RELATIVE TO THE STATE AND AMOUNT OF THE HABITAT, INCLUDING CARRYING CAPACITY LIMITS

DENSITY DEPENDENCE AND CARRYING CAPACITY

More than most fishes, American eels are influenced by their habitat because of the relationship between their highly variable life history characteristics and habitat features, including habitat-mediated impacts on growth and the determination of gender. American eels are considered habitat generalists because of their use of a wide variety of freshwater and saltwater habitats across a broad geographic range (Tesch 2003). It is unlikely that any specific habitat features are limiting any life stage given the vast areas of habitat available for each life stage and current population levels. That said, at finer spatial scales there is evidence in the literature for density dependent effects in the European Eel at various life stages (e.g., Völlestad and Jonsson 1988; DeLeo and Gatto 1996; Edeline et al. 2007; Acou et al. 2011). For example, there is some evidence for density-dependent mortality in glass eels, (Vøllestad and Jonsson 1988), though others argue that density-dependent effects occur primarily during the yellow stage (De Leo and Gatto 1996). High glass eel and elver densities are hypothesized to promote food competition, leading to density-dependent upstream dispersal (Feunteun et al. 2003; Edeline et al. 2007). A number of studies have documented density-dependent growth impacts in yellow eels, indicating that habitat can become limiting for this life stage (Völlestad and Jonsson 1988; De Leo and Gatto 1996; Acou et al. 2011). Acou et al. (2011) suggest that carrying capacity can be reached in European eels at densities of > 0.4 eels/m^2 or at biomass levels of 14.1 g/m^2; at these thresholds populations become male dominated, eels are spatially distributed to minimize competition, and there are growth and mortality impacts.

While marine and estuarine habitats remain largely intact, access to freshwater habitats have been greatly reduced in some areas (see above). Acou et al. (2011) indicate that the carrying capacity effects observed in their study were exacerbated by barriers. Barriers influence the density of American eels, with high densities occurring below impassable or semi-impassable barriers (Wiley et al. 1994; Lloyst 2012). There is evidence for density-dependent reductions in growth (Stacey 2013) and change in habitat use (Lloyst 2012) in American eels in high-density areas below barriers in the Lake Ontario watershed.

INFLUENCE OF HABITAT ON LIFE HISTORY CHARACTERISTICS

Sex Determination

There is substantial support that sex determination in temperate eels, including the American Eel, is mediated by habitat and density, though finding a unifying theory has proven difficult (Davey and Jellyman 2005). There are general geographic and habitat-based patterns, with more male-dominated locations in the southern part of the range and more female-dominated locations in the northern part of the range and more males in lotic and more females in lentic (reviews by Davey and Jellyman 2005; Vélez-Espino and Koops 2010). Gonadal development occurs during the yellow phase and sexual differentiation is generally initiated by 200 mm and is usually concluded by 350 mm total length (Davey and Jellyman 2005). Davey and Jellyman

(2005) proposed that gender was primarily determined by individual growth rates during the first few months of continental life, with females having higher initial growth rates than males. Similarly, Melia et al. (2006) and Huertas and Cerdà (2006) postulated that sex determination in the European Eel may be influenced by environmental and social conditions such as growth, water temperature and eel densities. In contrast, recent studies have suggested that eel sex determination may be a predisposed trait, dictated by a combination of genetic factors and environmental selection pressures faced by leptocephali and glass eels (Côté et al. 2009; Gagnaire et al. 2012; Stacey 2013). Ultimately, it is difficult to separate density effects from other factors such as sex-linked upstream migration patterns, habitat selection and genetic predisposition (Jessop 2010).

Growth

As mentioned earlier, yellow-phase American eels display three broad migration patterns; 1) eels that migrate into, and reside in, freshwater until maturity, 2) eels that remain in estuaries and nearshore coastal areas and never enter freshwater, and 3) eels migrating back and forth between these freshwater and marine habitats (Morrison et al. 2003; Lamson et al. 2006; Thibault et al. 2007a; Jessop et al. 2008; McCleave and Edeline 2009). It is thought that these migrations between freshwater and estuarine habitats are possibly seasonal in nature to take advantage of higher overwinter survival in freshwater and higher production in brackish water (Thibault et al. 2007a). There is growing evidence that brackish water habitats are more productive for yellow-stage American Eel. Yellow eels in brackish water are thought to grow faster, mature earlier, and outmigrate as silver eels sooner (Helfman et al. 1987; Morrison et al. 2003; Lamson et al. 2009).

RESIDENCE REQUIREMENTS FOR EEL

The *Species at Risk Act* defines a residence as:

“a dwelling-place, such as a den, nest or other similar area or place, that is occupied or habitually occupied by one or more individuals during all or part of their life cycles, including breeding, rearing, staging, wintering, feeding or hibernating”.

American eels at temperate latitudes are quiescent in the substrate during winter. In the southern Gulf of St. Lawrence, winter mud burrows can be readily located just before and just after the period of ice cover by the presence of fist-sized depressions on the bottom, which mark the entrance to the burrow. Tomie (2012) overwintered American eels in tanks with mud or cobble bottoms that were fed with water pumped from an adjacent river. Eels were largely immobile during the winter, lying without apparent movement in the same cavity for extended periods. However, occasional movements or departures from the wintering cavity were noted. Some eels wintering in southern Gulf of St. Lawrence bays and estuaries excavate wintering burrows in shallow areas of the bottom that appear relatively featureless, while others winter in areas of fresh-water seepages. These seepages are consistently used by eels and many are traditional sites of winter spear fisheries.

As some eels construct mud burrows with multiple entrances/exits, these burrows were evaluated against the definition of a residence to determine their potential consideration as a residence for American eels. Key questions in whether eel wintering burrows qualify as residences according to the above definition include whether a structure is required, and whether the residence has some degree of permanency. Burrows used by American eels in the southern Gulf of St. Lawrence are made of soft sediment and probably disappear by infilling within days or weeks of being vacated by an eel. Given that wintering burrows have some degree of structure, at least when they are occupied by eels, and that the same burrow is used for an extended period by an eel, it is possible that wintering burrows may meet the definition for residence under the *Species at Risk Act*.

LITERATURE CITED

Aarestrup, K., Økland, F., Hansen, M.M., Righton, D., Gargan, P., Castonguay, M., Bernatchez, L., Howey, P., Sparholt, H., Pedersen, M.I., and McKinley, R.S., 2009. Oceanic spawning migration of the European Eel (Anguilla anguilla). Science 325: 1660.

Acou, A., Rivot, E., van Gils, J.A., Legault, A., Ysnel, F., and Feunteun, E. 2011. Habitat carrying capacity is reached for the European eel in a small coastal catchment: evidence and implications for managing eel stocks. Freshw. Biol. 56: 952–968.

Barbin, G.P., Parker, S.J., and McCleave, J.D. 1998. Olfactory clues play a critical role in the estuarine migration of silver-phase American eels. Env. Biol. Fishes 53: 283–291.

Barbin, G.P., and Krueger, W.H. 1994. Behaviour and swimming performance of elvers of the American Eel, Anguilla rostrata, in an experimental flume. J. Fish Biol. 45: 111–121.

Barila, T.Y., and Stauffer, Jr., J.R. 1980. Temperature behavioral responses of the American eel, Anguilla rostrata (LeSueur), from Maryland. Hydrobiologia 74: 49–51.

Barker, D.B. 1997. Development of metazoan parasite communities in the American eel, Anguilla rostrata: patterns, processes and applicability as biological tags. Thesis (Ph.D.) Dalhousie University, Halifax, Nova Scotia.

Béguer-Pon, M., Benchetrit, J., Castonguay, M., Aarestrup, K., Campana, S.E., Stokesbury, M., and Dodson, J.J. 2012. Shark predation on migrating adult American eels (*Anguilla rostrata*) in the Gulf of St. Lawrence. PLoS ONE 7: e46830. doi:10.1371/journal.pone.0046830.

Béguer-Pon, M., Castonguay, M., Benchetrit, J., Hatin, D., Verreault, G., Mailhot, Y., Tremblay, V., Lefaivre, D., Legault, M., Stanley, D., and Dodson, J.J. Large scale migration patterns of silver American eels (*Anguilla rostrata*) from the St. Lawrence River to the Gulf using acoustic telemetry. Submitted for publication. Can. J. Fish. Aquat. Sci., April 2013.

Bernard, P., and Desrochers, D. 2007. Suivi des passes migratoires à anguille à la centrale de Beauharnois et au barrage de Chambly – 2007, [par] MILIEU inc., [pour] l’unité Environnement, division Production, Hydro-Québec. 81p.

Bradford, R.G. 2013. 2010 status of American eel (*Anguilla rostrata*) in Maritimes Region. DFO Can. Sci. Adv. Sec. Res. Doc. 2012/083. iv + 39 p.

Bradford, R.G., Carr, J.W., Page, F.H., and Whoriskey, F. 2009. Migration of silver American eels through a macrotidal estuary and bay. *In* Challenges for Diadromous Fishes in a Dynamic Global Environment. Edited by A. Haro, T. Avery, K. Beal, J. Cooper, R. Cunjak, M. Dadswell, R. Klauda, C. Moffit, R. Rulifson and K. Smith. Am. Fish. Soc. Symp. 69: 275–292.

Busch, W.-D.N., Lary, S.J., Castiglione, C.M., and McDonald, R. 1998. Distribution and availability of Atlantic coast freshwater habitats for American eel (*Anguilla rostrata*). United States Fish and Wildlife Service Administrative Report 98-2, Amherst, New York.

Byer, J.D., Alaee, M., Brown, R.S., Lebeuf, M., Backus, S., Keir, M., Pacepavicius, G., Casselman, J., Belpaire, C., Oliveira, K., Verreault, G., and Hodson, P.V. 2013a. Spatial trends of dioxin-like compounds in Atlantic anguillid eels. Chemosphere 91: 1439-1446.

Byer, J.D., Lebeuf, M., Alaee, M., Brown, R.S., Trottier, S., Backus, S., Keir, M., Couillard, C.M., Casselman, J., and Hodson, P.V. 2013b. Spatial trends of organochlorinated pesticides, polychlorinated biphenyls and polybrominated diphenyl ethers in Atlantic *Anguillid* eels. Chemosphere 90: 1719-1728.

Cairns, C.M. 2009. Population ecology of yellow-phase American eels (*Anguilla rostrata*) in the St. Jones River, Deleware. Thesis (M.Sc.) Delaware State University, Dover, Delaware.

Cairns, D.K., Shiao, J.C., Iizuka, Y., Tzeng, W.-N., and MacPherson, C.D. 2004. Movement patterns of American eels in an impounded watercourse, as indicated by otolith microchemistry. N. Am. J. Fish. Manag. 24: 452–458.

Cairns, D.K., Tremblay, V., Caron, F., Casselman, J.M., Verreault, G., Jessop, B.M., de Lafontaine, Y., Bradford, R.G., Verdon, R., Dumont, P., Mailhot, Y., Zhu X., Mathers, A., Oliveira, K., Benhalima, K., Dietrich, J., Hallett, J.A., and Lagacé, M. 2008. American eel abundance indicators in Canada. Can. Data Rep. Fish. Aquat. Sci. No. 1207. 78 p.

Cairns, D.K., Secor, D.A., Morrison W.E., and Hallett, J.A. 2009. Salinity-linked growth in anguillid eels and the paradox of temperate-zone catadromy. J. Fish Biol. 74: 2094–2114.

Cairns, D.K., Dutil, J.-D., Proulx, S., Mailhiot, J.D., Bédard, M.-C., Kervella, A., Godfrey, L.G., O'Brien, E.M., Daley, S.C., Fournier, E., Tomie, J.P.N., and Courtenay, S.C. 2012. An atlas and classification of aquatic habitat on the east coast of Canada, with an evaluation of usage by the American eel. Can. Tech. Rep. Fish. Aquat. Sci. No. 2986. 103 p.

Cairns, D.K., Chaput, G., Poirier, L.A., Avery, T.S., Castonguay, M., Mathers, A., Bradford, R.G., Pratt, T., Verreault, G., Clarke, K., Veinnot, G., and Bernatchez, L. 2014. Recovery Potential Assessment for the American Eel (*Anguilla rostrata*) for eastern Canada: life history, distribution, status indicators, and demographic parameters. DFO Can. Sci. Adv. Sec. Res. Doc. 2013/134.

Caron, F., Verreault, G., and Rochard, E. 2003. Estimation of the population size, exploitation rate, and escapement of silver-phase American eels in the St. Lawrence watershed. *In* Biology, Management, and Protection of Catadromous Eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp 33: 235–242.

Casselman, J.M. 2003. Dynamics of resources of the American eel*, Anguilla rostrata*: declining abundance in the 1990s. *In* Eel Biology. Edited by K. Aida, K. Tsukamoto, and K. Yamauchi. Springer-Verlag, Tokyo, p. 255–274.

Castonguay, M., and McCleave, J.D. 1987. Vertical distributions, diel and ontogenetic vertical migrations and net avoidance of leptocephali of Anguilla and other common species in the Sargasso Sea. J. Plankton Res. 9: 195–214.

Castonguay, M**.**, Hodson, P.V., Couillard, C.M., Eckersley, M.J., Dutil J.-D., and Verreault, G. 1994. Why is recruitment of the American eel declining in the St. Lawrence River and Gulf? Can. J. Fish. Aquat. Sci. 51: 479–488.

Chaput, G., Locke, A., and Cairns, D. 1997. Status of American eel (*Anguilla rostrata*) for the Southern Gulf of St. Lawrence. *In* The American eel in eastern Canada: stock status and management strategies. Edited by R.H. Petersen. Can. Tech. Rep. Fish. Aquat. Sci. 2196, Québec City. p. 69–93.

Chaput, G., and Bradford, R.G. 2003. American shad (*Alosa sapidissima*) in Atlantic Canada DFO Canadian Stock Assessment Secretariat Research Document 2003/009.

COSEWIC. 2012. COSEWIC assessment and status report on the American *Eel Anguilla rostrata* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xii + 109 p.

Côté, C.L., Castonguay, M., Verreault, G., and Bernatchez, L. 2009. Differential effects of origin and salinity rearing conditions on growth of glass eels of the American eel *Anguilla rostrata*: implications for stocking programmes. J. Fish Biol. 74: 1934–1948.

Cowardin, L.M., Carter, V., Golet, F.C., and LaRoe, E.T. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service FWS/OBS 79/31. As reprinted in 1992. 131 p.

Creutzberg, F. 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. Neth. J. Sea Res. 1: 257–338.

Dahl, T.E., Dick, J., Swords, J., and Wilen, B.O. 2009. Data collection requirements and procedures for mapping wetland, deepwater and related habitats of the United States. United States Fish and Wildlife Service, Division of Habitat, Madison WI. 85 p.

Davey, A.J.H., and Jellyman, D.J. 2005. Sex determination in freshwater eels and management options for manipulation of sex. Rev. Fish Biol. Fish. 15: 37–52.

Davis, D.S., and Browne, S.H. 1997. The Natural History of Nova Scotia, Vol. 1. Topics and Habitats. Nimbus Publishing, Halifax, Nova Scotia, Canada.

Deelder, D.L. 1952. On the migration of the elver (Anguilla vulguris Turt.) at sea. J Cons. int. Explor. Mer 18: 187–218.

de Lafontaine, Y., Lagacé, M., Gingras, F., Labonté, D., Marchand, F., and Lacroix, E. 2009. Decline of the American eel in the St. Lawrence River: Effects of local hydroclimatic conditions on CPUE indices. *In* Eels at the Edge: Science, Status, and Conservation Concerns. Edited by J.M. Casselman and D.K. Cairns. Am. Fish. Soc. Symp 58: 207-228.

De Leo, G.A., and Gatto, M. 1996 Trends in vital rates of European eel: evidence for density dependence? Ecol. Appl. 6: 1281–1294.

Denoncourt, C.E., and Stauffer, Jr., J.R. 1993. Feeding selectivity of the American eel *Anguilla rostrata* (LeSueur) in the upper Delaware River. Am. Midl. Nat. 129: 301–308.

Dutil, J -D., Giroux, A., Kemp, A., Lavoie, G., and Dallaire, J.P. 1988. Tidal influence on movements and on daily cycle of activity of American eels. Trans. Am. Fish. Soc. 117: 488–494.

Dutil, J.-D., Michaud, M., and Giroux, A. 1989. Seasonal and diel patterns of stream invasion by American eels (*Anguilla rostrata*) in the northern Gulf of St. Lawrence. Can. J. Zool. 67: 182–188.

Dutil, J.-D., Dumont, P., Cairns, D.K., Galbraith, P.S., Verreault, G., Castonguay, M., and Proulx, S. 2009. *Anguilla rostrata* glass eel migration and recruitment in the estuary and Gulf of St. Lawrence. J. Fish Biol. 74: 1970–1984.

Edeline, E., Dufour, S. and Elie, P. 2005. Role of glass eel salinity preference in the control of habitat selection and growth plasticity in *Anguilla anguilla*. Mar Ecol Prog Ser 304: 191–199.

Edeline, E., Lambert, P., Rigaud, C., and Elie, P. 2006. Effects of body condition and water temperature on *Anguilla anguilla* glass eel migratory behavior. J. Exp. Mar. Biol. Ecol. 331: 217–225.

Edeline, E., Beaulaton, L., Le Barh, R., and Elie, P. 2007. Dispersal in metamorphosing juvenile eel *Anguilla anguilla*. Mar Ecol Prog Ser 344: 213–218.

Facey, D.E., and LaBar, G.W. 1981. Biology of American eels in Lake Champlain, Vermont. Trans. Am. Fish. Soc. 110: 396–402.

Facey, D.E., and Van den Avyle, M.J. 1987. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) –American eel. U.S. Fish and Wildlife Service Biological Report No. 82(11.74), and U.S. Army Corps of Engineers Report No. TR EL-82-4, Washington, DC.

Feunteun, E., Laffaille, P., Robinet, T., Briand, C., Baisez, A., Olivier, J.M., and Acou, A. 2003. A review of upstream migration and movements in inland waters by anguillid eels. Towards a general theory. *In* Eel Biology. Edited by K. Aida, K. Tsukamoto, and K. Yamauchi. Springer-Verlag, Tokyo. p. 191–213.

Fielding, G. 2011. Barriers to fish passage in Nova Scotia. The evolution of water control barriers in Nova Scotia’s watershed. Thesis (ENVS Honours) Dalhousie University, Halifax, Nova Scotia.

Fischer, P., and Eckmann, R. 1997. Spatial distribution of littoral fish species in a large European lake, Lake Constance, Germany. Archiv für Hydrobiolie 140: 91–116.

Ford, T.E., and Mercer, E. 1986. Density, size distribution and home range of American eels, *Anguilla rostrata*, in a Massachusetts salt marsh. Env. Biol. Fishes 17: 309–314.

Fricke, H., and Tsukamoto, K. 1998. Seamounts and the mystery of eel spawning. Naturwissenschaften 85: 290–291.

Gagnaire, P.A., Normandeau, E., Côté, C., Hansen, M.M., and Bernatchez, L. 2012. The effect of spatially varying selection on locally adaptive alleles in the panmictic American eel (*Anguilla rostrata*). Genetics 190: 725–736.

Geer, P.J. 2003. Distribution, relative abundance, and habitat use of American eel *Anguilla rostrata* in the Virginia portion of the Chesapeake Bay. Am. Fish. Soc. Symp. 35: 101–115.

Geeraerts, C., and Belpaire, C. 2010. The effects of contaminants in European eel: A review. Ecotoxicology 19: 239–266.

Greene, K.E., Zimmerman, J.L., Laney, R.W., and Thomas-Blate, J.C. 2009. Atlantic coast diadromous fish habitat: A review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission Habitat Management Series No. 9, Washington, D.C. 465 p.

Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. Trends Ecol. Evol. 17: 22–27.

Guignion, D.L. 2009. A conservation strategy for Atlantic salmon in Prince Edward Island. Prince Edward Island Council of the Atlantic Salmon Federation, Charlottetown. 168 p.

Hallett, J.A. 2013. Densities, populations, and exploitation rates of American eels in the southern Gulf of St. Lawrence, from glass bottom boat surveys. Thesis (M.Sc.) University of New Brunswick, Fredericton, New Brunswick.

Haro, A.J. 1991. Thermal preferenda and behavior of Atlantic eels (genus *Anguilla*) in relation to their spawning migration. Env. Biol. Fishes 31: 171–184.

Haro, A.J., and Krueger, W.H. 1988. Pigmentation, size and migration of elvers (*Anguilla rostrata* (LeSueur)) in a coastal Rhode Island stream. Can. J. Zool. 66: 2528–2533.

Haro, A.J., and Krueger, W.H. 1991. Pigmentation, otolith rings, and upstream migration of juvenile American Eels (*Anguilla rostrata*) in a coastal Rhode Island stream. Can. J. Zool. 69: 812–814.

Haro, A., Richkus, W., Whalen, K., Hoar, A., Busch, W.D., Lary, S., Brush, T., and Dixon, W. 2000. Population decline of the American eel: implications for research and management. Fisheries 25: 7–16.

Hedger, R.D., Dodson, J.J., Hatin, D., Caron, F., and Fournier, D. 2010. River and estuary movements of yellow-stage American eels *Anguilla rostrata*, using a hydrophone array. J. Fish Biol. 76: 1294–311.

Helfman, G.S., Stoneburner, D.L., Bozeman, E.L., Christian, P.A., and Whalen, R. 1983. Ultrasonic telemetry of American eel movements in a tidal creek. Trans. Am. Fish. Soc. 112: 105–110.

Helfman, G.S., Bozeman, E.L., and Brothers, E.B. 1984. Size, age, and sex of American eel in a Georgia river. Trans. Am. Fish. Soc. 113: 132–141.

Helfman, G.S., Facey, D.E., Hales, Jr., L.S., and Bozeman, Jr., E.L. 1987. Reproductive ecology of the American eel. Am. Fish. Soc. Symp. 1: 42–56.

Huertas, M., and Cerdà, J. 2006. Stocking density at early developmental stages affects growth and sex ratio in the European eel (*Anguilla anguilla*). Biol. Bull. 211: 286–296.

ICES. 2009. Report of the ICES Study Group on anguillid eels in saline waters (SGAESAW). ICES CM/DFC:06. 183 p.

Jessop, B.M. 1987. Migrating American eels in Nova Scotia. Trans. Am. Fish. Soc. 116: 161–170.

Jessop, B.M. 1998. Geographic and seasonal variation in biological characteristics of American eel elvers in the Bay of Fundy area and on the Atlantic coast of Nova Scotia. Can. J. Zool. 76: 2172–2185.

Jessop, B.M. 2000. Estimates of population size and instream mortality rate of American eel elvers in a Nova Scotia river. Trans. Am. Fish. Soc. 129: 514–526.

Jessop, B.M. 2003. Annual variability in the effects of water temperature, discharge, and tidal stage on the migration of American Eel elvers from estuary to river. *In* Biology, Management, and Protection of Catadromous Eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp. 33: 3–16.

Jessop, B.M. 2010. Geographic effects on American eel (*Anguilla rostrata*) life history characteristics and strategies. Am. Fish. Soc. Symp. 67: 326–346.

Jessop, B.M., Shiao, J.C., Iizuka, Y., and Tzeng, W.-N. 2006. Migration of juvenile American eels *Anguilla rostrata* between freshwater and estuary as revealed by otolith microchemistry. Mar. Ecol. Prog. Ser. 310: 219–233.

Jessop, B.M., Cairns, D.K., Thibault, I., and Tzeng, W.-N. 2008. Life history of American eel *Anguilla rostrata*: new insights from otolith microchemistry. Aquatic Biol 1: 205–216.

Jessop, B.M., Shiao, J.C., and Iizuka, Y. 2009. Life history of American eels from western Newfoundland. Trans. Am. Fish. Soc. 138: 861–871.

Jessop, B.M., and Harvie, C.J. 2003. A CUSUM analysis of discharge patterns from a hydroelectric dam and discussion of potential effects on the upstream migration of American eel elvers. Can. Tech. Rep. Fish. Aquat. Sci. 2454. v + 28 pp.

Kidd, S.D., Curry, A., and Munkittrick, K.R. 2011. The Saint John River: A State of the Environment Report. Canadian Rivers Institute, University of New Brunswick. Fredericton. 142 pp.

Kleckner, R C., and McCleave, J.D. 1982. Entry of migrating American eel leptacephali into the Gulf Stream system. Helgolander Meeresun 35: 329–339.

Kleckner, R.C., and McCleave, J.D. 1985. Spatial and temporal distribution of American Eel larvae in relation to North Atlantic Ocean current systems. Dana 4: 67–92.

Kleckner, R.C., and McCleave, J.D. 1988. The northern limit of spawning by Atlantic eels (*Anguilla* spp.) in the Sargasso Sea in relation to thermal fronts and surface water masses. J. Mar. Res. 46: 647–667.

Kleckner, R.C., McCleave, J.D., and Wippelhauser, G.S. 1983. Spawning of American eel, *Anguilla rostrata*, relative to thermal fronts in the Sargasso Sea. Env. Biol. Fishes 9: 289–293.

Knights, B., and White, E.M. 1998. Enhancing immigration and recruitment of eels: the use of passes and associated trapping systems. Fish. Manage. Ecol. 112: 111–116.

LaBar, G.W., and Facey, D.E. 1983. Local movements and inshore population sizes of American eels in Lake Champlain, Vermont. Trans. Am. Fish. Soc. 112: 111–116.

Lamson, H.M. 2005. Movement patterns and growth of American Eels (*Anguilla rostrata*) between salt and freshwater, based on otolith microchemisty. Thesis (M.Sc.) University of New Brunswick, Fredericton, New Brunswick.

Lamson, H.M., Shiao, J.-C., Lizuka, Y., Tzeng, W.-N., and Cairns, D.K. 2006. Movement patterns of American eels (*Anguilla rostrata*) between salt and fresh water in a coastal watershed, based on otolith microchemistry. Mar. Biol. 149: 1567–1576.

Lamson, H.M., Cairns, D.K., Shiao J.-C., Iizuka, Y., and Tzeng, W.-N. 2009. American eel, *Anguilla rostrata*, growth in fresh and salt water: implications for conservation and aquaculture. Fish. Manage. Ecol. 16: 306–314.

Lary, S.J., and Busch, W.-D.N. 1997. American eel (*Anguilla rostrata*) in Lake Ontario and its tributaries: Distribution, abundance, essential habitat and restoration requirements. United States Fish and Wildlife Service Administrative Report 97-1. Amherst, New York.

Legault, A. 1988. Le franchissement des barrages par l’escalade de l’anguille: étude en Sèvre Niortaise. Bull. Fr. Peche Piscic. 308: 1–10.

Leonard, G.H., Ewanchuk, P.J., and Bertness, M.D. 1999. How recruitment, intraspecific interactions, and predation control species borders in a tidal estuary. Oecologia 118: 492–502.

Lloyst, M.H. 2012. The distribution and habitat associations of stocked American Eel, *Anguilla rostrata*, in Lake Ontario and the Upper St. Lawrence River. Thesis (M.Sc.) Trent University, Peterborough, Ontario.

Lookabaugh, P.S., and Angermeier, P.L. 1992. Diet patterns of American eel, *Anguilla rostrata*, in the James River drainage, Virginia. J. Freshw. Ecol. 7: 425–431.

MacFarlane, R.E. 1999. An evaluation of the potential impacts of some Prince Edward Island impoundments on salmonid habitat. Thesis (M.Sc.) Acadia University, Wolfville, Nova Scotia.

MacGregor, R., Casselman, J., Greig, L., Allen, W.A., McDermott, L., and Haxton, T. 2010. Draft recovery strategy for the American Eel (*Anguilla rostrata*) in Ontario. Ontario Recovery Strategy Series. Prepared for Ontario Ministry of Natural Resources, Peterborough, Ontario. vii+78 pp.

Machut, L.S., Limburg, K.E., Schmidt, R.E., and Dittman, D. 2007. Anthropogenic impacts on American Eel demographics in Hudson River tributaries, New York. Trans. Am. Fish. Soc. 136: 1699–1713.

Martin, M.H. 1995. The effects of temperature, river flow, and tidal cycles on the onset of glass eel and elver migration into freshwater in the American Eel. J. Fish Biol. 46: 891–902.

McCleave, J.D. 2003. Spawning areas of Atlantic eels. *In* Eel Biology. Edited by K. Aida, K. Tsukamoto, and K. Yamauchi. Springer-Verlag, Tokyo, p.141–156.

McCleave, J.D., Kleckner, R.C., and Castonguay, M. 1987. Reproductive sympatry of American and European eels and implications for migration and taxonomy. Am. Fish. Soc. Symp. 1: 286-297.

McCleave, J.D., and Edeline, E. 2009. Diadromy as a conditional strategy: Patterns and drivers of eel movements in continental habitats. Am. Fish. Soc. Symp. 69: 97–119.

McGrath, K.J., Desrocher, D., Fleury, C., and Dembeck IV, J.W. 2003a. Studies of upstream migrant American Eels at the Moses-Saunders Power Dam on the St. Lawrence River near Massena, New York. *In* Biology, Management, and Protection of Catadromous Eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp. 33: 153–166.

McGrath, K.J., Bernier, J., Ault, S., Dutil, J.-D., and Reid, K. 2003b. Differentiating downstream migrating American Eels *Anguilla rostrata* from resident eels in the St. Lawrence River. *In* Biology, Management, and Protection of Catadromous Eels. D.A. Dixon. Am. Fish. Soc. Symp. 33: 315–327.

Medcof, J.C. 1969. Fishermen's reports of freshwater and saltwater migrations of Nova Scotia eels (*Anguilla rostrata*). Can. Field-Nat. 83: 132–138.

Meffe, G.K., and Sheldon, A.L. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. Am. Midl. Nat. 120: 225–240.

Melia, P., Bevacqua, D., Crivelli, A.J., Panfili, J., De Leo, G.A., and Gatto, M. 2006. Sex differentiation of the European eel in brackish and freshwater environments: a comparative analysis. J. Fish Biol. 69: 1228–1235.

Miller, M.J., Kimura, S., Friedland, K.D., Knights, B., Kim, H., Jellyman, D.J., and Tsukamoto, K. 2009. Review of ocean-atmospheric factors in the Atlantic and Pacific oceans influencing spawning and recruitment of anguillid eels. *In* Challenges for Diadromous Fishes in a Dynamic Global Environment. Edited by A. Haro, T. Avery, K. Beal, J. Cooper, R. Cunjak, M. Dadswell, R. Klauda, C. Moffit, R. Rulifson, and K. Smith. Am. Fish. Soc. Symp. 69: 231–249.

Mills, E.L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J.A., Johannsson, O.E., Lantry, B.F., Makarewicz, J.C., Millard, E.S., Munawar, I.F., Munawar, M., O'Gorman, R., Owens, R.W., Rudstam, L.G., Schaner, T., and Stewart, T.J. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Can. J. Fish. Aquat. Sci. 60: 471–490.

Morrison, W.E., and Secor, D.H. 2003. Demographic attributes of yellow-phase American eels (*Anguilla rostrata*) in the Hudson River estuary. Can. J. Fish. Aquat. Sci. 60: 1487–1501.

Morrison, W.E., Secor, D.H., and Piccoli, P.M. 2003. Estuarine habitat use by Hudson River American eels as determined by otolith strontium: calcium ratios. *In* Biology, management, and protection of catadromous eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp. 33: 87–99.

Munk, P., Hansen, M.M., Maes, G.E., Nielsen, T.G., Castonguay, M., Riemann, L., Sparholt, H., Als, T.D., Aarestrup, K., Andersen, N.G., and Bachler, M. 2010. Oceanic fronts in the Sargasso Sea control the early life and drift of Atlantic eels**.** Philos. Trans. R. Soc. Lond., B 277: 3593–3599.

Nicholls, T. 2011. Draft report on the potential impacts on American Eel habitat in Newfoundland and Labrador. Department of Environment and Conservation, Government of Newfoundland and Labrador and Fisheries and Oceans Canada, Government of Canada. v + 39 pp.

Nyman, L. 1972. Some effects of temperature on eel (Anguilla) behaviour. Inst. of Freshw. Res. (Drottningholm, Sweden) 52: 90–102.

Ogden, J.C. 1970. Relative abundance, food habits, and age of the American eel, *Anguilla rostrata* (LeSueur), in certain New Jersey streams. Trans. Am. Fish. Soc. 99: 54-59.

Oliveira, K. 1999. Life history characteristics and strategies of American eel, *Anguilla rostrata*, in four rivers in Maine, U.S.A. Can. J. Fish. Aquat. Sci. 56: 795–802.

Oliveira, K., and Hable, W.E. 2010. Artificial maturation, fertilization, and early development of the American Eel (*Anguilla rostrata)*. Can. J. Zool. 88: 1121–1128.

Parker, S.J., and McCleave, J.D. 1997. Selective tidal stream transport by American eels during homing movements and estuarine migration. J. Mar. Biol. Ass. U. K. 77: 871–889.

Pratt, T.C., and Threader, R.W. 2011. Preliminary evaluation of a large-scale American eel conservation stocking experiment. N. Am. J. Fish. Manag.31: 619–628.

Richkus, W.A., and Dixon, D.A. 2003. Review of research and technologies on passage and protection of downstream migrating catadromous eels at hydroelectric facilities. *In* Biology, Management, and Protection of Catadromous Eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp. 33: 377–388.

Robinet, T., and Feunteun, E. 2002. Sublethal effects of exposure to chemical compounds: a cause for the decline in Atlantic eels. Ecotoxicology 11: 265–277.

Ruggles, C.P., and Watt, W.D. 1975. Ecological changes due to hydroelectric development on the Saint John River. J. Fish. Res. Board Can. 32: 161–170.

Rulifson, R.A., Cahoon, C., and Cudney, J.L. 2004. Critical habitat assessment and population demographics of the American eel fishery in Northwestern Pamlico Sound, North Carolina. Final Report for the North Carolina Sea Grant Fishery Resource Grant Program, Project No. 02-EP-13.

Sadler, K. 1979. Effects of temperature on the growth and survival of the European eel, *Anguilla anguilla* L. J. Fish Biol. 15: 499–507.

Schmidt, J. 1922. The breeding places of the eel. Philos. Trans. R. Soc. Lond., B 211: 179–208.

Schmidt, J. 1935. Danish eel investigations during 25 years 1905-1930. Carlsberg Foundation, Copenhagen. 16 p.

Schulze, T., Kahl, U., Radke, R.J., and Benndorf, J. 2004. Consumption, abundance and habitat use of *Anguilla anguilla* in a mesotrophic reservoir. J. Fish Biol. 65: 1543–1562.

Solomon, D.J., and Beach, M.H. 2004. Fish pass design for eel and elver (*Anguilla anguilla*). R&D Technical Rport W2-070/TR1. Environment Agency, United Kingdom.

Sorensen, P.W. 1986. Origins of the freshwater attractant(s) of migrating elvers of the American eel, *Anguilla rostrata*. Env. Biol. Fishes 17: 185–200.

Sorensen, P.W., and Bianchini, M.L. 1986. Environmental correlates of the freshwater migration of elvers of the American eel in a Rhode Island brook. Trans. Am. Fish. Soc. 115: 258–268.

Stacey, J.A. 2013. The life history strategy, growth, body condition, and diet of stocked American eel (*Anguilla rostrata*) in the upper St. Lawrence River and Lake Ontario. Thesis (M.Sc.) Trent University, Peterborough, Ontario.

Steinbach, P. 2006. Expertise de la franchissabilité des ouvrages hydrauliques transversaux par l'anguille dans le sens de la montaison. Conseil Supérieur de La Pêche. Note méthodologique. 16 pp.

Tesch, F.-W. 1978. Telemetric observations on the spawning migration of the eel (*Anguilla anguilla*) west of the European continental shelf. Env. Biol. Fishes 3: 203–209.

Tesch, F.-W. 1995. Vertical movements of migrating silver eels (*Anguilla anguilla*) in the sea. Bull. Sea Fish Inst. 2: 24–30.

Tesch, F.-W. 2003. The eel: Biology and management of anguillid eels, 5th edition. Blackwell Science Ltd., Oxford, United Kingdom.

Thibault, I., Dodson, J.J., and Caron, F. 2007a. Yellow-stage American eel movements determined by microtagging and acoustic telemetry in the St. Jean River watershed, Gaspé, Quebec, Canada. J. Fish Biol. 71: 1095–1112.

Thibault, I., Dodson, J.J., Caron, F., Tzeng, W.-N., Iizuka, Y., and Shiao, J.C. 2007b. Facultative catadromy in the American eel: testing the conditional strategy hypothesis. Mar. Ecol. Prog. Ser. 344: 219–229.

Thomas, J.C. 2006. American eel behavioral patterns in Silver Lake, Dover, Delaware. Thesis (MS) University of Delaware, Dover, Delaware.

Thrush, S.F., and Dayton, P.K. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annu. Rev. Ecol. Syst. 33: 449–473.

Tomie, J.P.N. 2012. The ecology and behaviour of substrate occupancy by the American Eel. Thesis (M.Sc.) University of New Brunswick, Fredericton, New Brunswick.

Tremblay, V., Cossette, C., Dutil, J.-D., Verreault, G., and Dumont, P. 2011. Assessment of upstream and downstream passability for eel at dams. Can. Tech. Rep. Fish. Aquat. Sci. 2912: x + 73 p.

Tsukamoto, K. 2006. Spawning of eels near a seamount. Nature 439: 929.

Tzeng, W.N., Wang, Y.T., and Wang, C.H. 1998. Optimal growth temperature of the American eel, *Anguilla rostrata* (Le Sueur). J. of the Fish. Soc. Taiwan 25: 111–115.

Veinott, G., and Clarke, K. 2011. Status of American Eel in Newfoundland and Labrador Region: Prepared for the pre-COSEWIC and eel zonal advisory process (ZAP), Ottawa, August 31 to Sept 3, 2010. DFO Can. Sci. Adv. Sec. Res. Doc. 2010/138. iv + 20 p.

Vélez-Espino, L.A., and Koops, M.A. 2009. A synthesis of the ecological processes influencing variation in life history and movement patterns of American eel: towards a global assessment. Rev. Fish Biol. Fish. 20: 163–186.

Verdon, R., and Desrochers, D. 2003. Upstream migratory movements of American Eel *Anguilla rostrata* between the Beauharnois and Moses-Saunders power dams on the St. Lawrence River. In: Dixon, D.A. (Ed), Biology, Management, and Protection of Catadromous Eels. Am. Fish. Soc. Symp. 33: 139–151.

Verdon, R., Desrochers, D., and Dumont, P. 2003. Recruitment of American eels in the Richelieu River and Lake Champlain: provision of upstream passage as a regional-scale solution to a large-scale problem. *In* Biology, Management, and Protection of Catadromous Eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp. 33: 125–138

Verreault, G., Pettigrew, P., Tardif, R., and Pouliot, G. 2003. The exploitation of the migrating silver American eel in the St. Lawrence River Estuary, Québec, Canada. *In* Biology, Management, and Protection of Catadromous Eels. Edited by D.A. Dixon. Am. Fish. Soc. Symp. 33: 235–234.

Verreault, G., Dumont, P., and Mailhot, Y. 2004. Habitat losses and anthropogenic barriers as a cause of population decline for American eel (*Anguilla rostrata*) in the St. Lawrence watershed, Canada. ICES CM 2004/S:04. 2004 ICES Annual Science Conference held September 22-25, Vigo, Spain. 12 p.

Vøllestad, L.A., and Jonsson, B. 1988. A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: evidence for density-dependent mortality, and development of a model for predicting yield. J. Anim. Ecol. 57: 983–997.

Walsh, P.J., Foster, G.D., and Moon, T.W. 1983. The effects of temperature on metabolism of the American eel *Anguilla rostrata* (LeSueur): Compensation in the summer and torpor in the winter. Physiol. Zool. 56: 532–540.

Warner, K. 1965. Fishery Management in the Fish River. Maine Department of Inland Fish and Game, Fisheries Research Bulletin 6. 52 pp.

Wells, P.G. 1999. Environmental Impact of Barriers on Rivers Entering the Bay of Fundy: Report of an ad hoc Environment Canada Working Group. Technical Report Series No. 334, Canadian Wildlife Service, Ottawa, ON. 43pp.

Wenner, C.A. 1973. Occurrence of American eels, *Anguilla rostrata*, in water overlying the eastern North America Continental Shelf. J. Fish. Res. Board Can. 30: 1752–1755.

Wiley, D.J., Morgan II, R.P., Hilderbrand, R.H., Raesly, R.L., and Shumway, D.L. 2004 Relations between physical habitat and American eel abundance in five river basins in Maryland. Trans. Am. Fish. Soc. 133: 515–526.

Wippelhauser, G.S., and McCleave, J.D. 1987. Precision of behavior of migrating juvenile American eels (*Anguilla rostrata*) utilizing selective tidal stream transport. ICES Mar. Sci. 44: 80–89.

Wuenschel, M.J., and Able, K.W. 2008. Swimming ability of eels (*Anguilla rostrata, Conger oceanicus*) at estuarine ingress: contrasting patterns of cross-shelf transport? Mar. Biol. 154: 775–786.

Yokouchi, K., Aoyama, J., Miller, M.J., McCarthy, T.K., and Tsukamoto, K. 2009. Depth distribution and biological characteristics of the European eel *Anguilla anguilla* in Lough Ennell, Ireland. J. Fish Biol. 74: 857–871.

Table 1. A summary of known American Eel habitat associations. Supporting documentation for the habitat features, functions and attributes can be found in the text in the section describing American Eel habitat by life stage.

Life Stage	Function	Features	Location	Attributes	
Silver eel (spawning)	Spawning; occurs from February through April	Sargasso Sea; approximately 19.2°N to 29°N and 52°W to 79°W, depending on location of temperature fronts	Marine	Temperature	>18-19°C
				Depth	Upper 300 m of water column
				Salinity	Up to 36.6 ppt
Egg	Egg incubation; occurs from February through April; egg stage duration is only a couple of days	Sargasso Sea; approximately 19.2°N to 29°N and 52°W to 79°W	Marine	Temperature	Not reported; hatching at 20°C in the laboratory
				Depth	Not reported; based on spawning and leptocephali depths likely in upper 300 m of water column
				Salinity	Not reported
Leptocephali	Early development, initial dispersal and migration; stage lasts a few months to a year	Open ocean in dominant currents (e.g., Gulf Stream)	Marine	Temperature	Not reported
				Depth	Found in upper 350 m of water column; diel vertical migrations occur with leptocephali found shallow (50-100 m depths) at night.
				Salinity	Not reported
Glass eel/elver	Dispersal and initial growth; stage lasts a few months, beginning earlier in the southern part of the range	Initially open ocean, with migration to nearshore coastal, estuarine and freshwater habitats	Marine	Temperature	Not reported
				Depth	Variable; mostly in upper 100 m
				Salinity	Not reported
			Estuarine	Temperature	Variable, high tolerance
				Salinity	Variable, high tolerance

Life Stage	Function	Features	Location	Attributes	
				Substrate	Coarse (interstitial spaces) or soft (burrowing) substrates for protection from tides and currents
				Diel and lunar cycle	Initially negatively phototactic; response diminishes over time
			Freshwater	Temperature	10-20°C, with most upstream migration occurring between these extremes
				Substrate	Coarse (interstitial spaces) or soft (burrowing) substrates for protection from tides and currents
				Velocity	Flows < 25-35 cm/sec; greater migrations occur with decreasing velocities
Yellow eel	Primary growth and continued dispersal; stage can last a few years to > 25 years	Nearshore coastal, estuarine, and freshwater habitats (streams, rivers and lakes); evidence for migration between the diverse habitat types	Marine	Temperature	Not reported
				Depth	Variable; captures include locations > 100 m in depth
				Salinity	Not reported
			Estuarine	Temperature	Wide tolerance (0-31°C; limited activity or torpor below 4°C
				Depth	Variable; captures include depths > 25 m
				Salinity	Variable; wide tolerance
				Substrate	Variable; possibly prefer soft substrates
			Freshwater	Temperature	Wide tolerance (0-31°C; limited activity or torpor below 8°C; preferred 17-20°C

Life Stage	Function	Features	Location	Attributes	
				Depth	Variable depth range; majority between 1-10 m
				Substrate	Variable; depends on body size
				Velocity	Variable
				Oxygen	Variable; not less than 4 mg/L
Silver eel (migrating)	Migration to spawning grounds, primarily in fall	Initially from yellow stage rearing locations (freshwater, estuarine and marine), then open ocean	Freshwater	Temperature	Variable; range between 10-20°C
				Depth	Variable; 4-10m
				Diel and lunar phase	Primarily at night; more active with new moon
				Velocity	Variable; high flow may trigger migration
			Estuarine	Temperature	Variable; 10-17°C
				Depth	Variable;
				Diel and lunar phase	Initiating early evening with migration primarily at night
				Substrate	Possible use of protective substrate on bottom during flood tides
			Marine	Temperature	8-12°C
				Depth	Variable; reported from 9-82 m. Diel vertical migration apparent in European eel with use of upper 250 m at night and 500 m during the day

Table 2. Extent of occurrence and area of occupancy (km²) of the American Eel from each National Freshwater Biogeographic Zone. Table is from COSEWIC (2012).

National Freshwater Biogeographic Zones (NFBZ)	Extent of occurrence (EO) (km²)*	Biological Area of occupancy (km²)
NFBZ10 (Great Lakes – Western (Upper) St. Lawrence)	391,515	97,400 (5.9%)
NFBZ9 (Eastern (Lower) St. Lawrence)	546,122	161,400 (9.8%)
NFBZ1 (Maritimes (New Brunswick, Nova Scotia, Prince Edward Island, and the central and southern parts of Québec's Gaspé Peninsula))	292,923	635,200 (38.4%)
NFBZ8 (Atlantic Islands (Newfoundland))	177,586	627,500 (38.0%)
NFBZ2 (Eastern Arctic (Labrador))	75,472	130,700 (7.9%)
Total	2,065,932	1,652,200 (100%)

*The Sum of EO by NFBZ does not add up to the Canadian total because of the method used to calculate EO. A minimum convex polygon is constructed around the points for each NFBZ or the entire Canadian range. Because of the geography of Eastern Canada, more area is encompassed for the entire Canadian range than for the sum of NFBZ-specific polygons (N. Mandrak, DFO, personal communication).

Table 3.The number of sites electrofished and the mean (± standard deviation) number of eels caught per 100 m^2 of habitat by year and sub-drainage of the Saint John River. The sub-drainages are displayed relative to their location (upstream or downstream) of Mactaquac Dam.

Year	Below Mactaquac						Above Mactaquac					
	Hammond		Keswick		Nashwaak		Meduxnekeag		Shikatehawk		Tobique	
	# sites	Mean	# sites	Mean	# sites	Mean	# sites	Mean	# sites	Mean	# sites	Mean
1992	-	-	4	2.4 (2.8)	5	0.6 (0.8)	4	0.0	2	0.0	3	0.0
1993	-	-	5	1.4 (1.5)	10	1.5 (1.4)	5	0.0	5	0.0	-	-
1994	4	1.9 (3.8)	5	0.0	14	0.5 (0.8)	5	0.0	5	0.0	5	0.0
1995	-	-	4	2.1 (1.3)	8	0.6 (0.9)	5	0.0	4	0.0	10	0.0
1996	4	0.8 (0.6)	4	0.9 (0.8)	9	1.4 (0.7)	4	0.0	5	0.0	18	0.01 (0.01)
1997	4	1.0 (0.6)	4	0.5 (0.3)	9	1.0 (0.7)	5	0.0	2	0.0	17	0.0
1998	4	0.5 (0.4)	3	1.6 (0.3)	13	1.2 (0.9)	5	0.0	4	0.0	17	0.0
1999	4	0.7 (0.4)	4	0.9 (0.6)	13	0.7 (0.7)	5	0.0	5	0.0	18	0.0
2000	2	0.0	3	0.2 (0.2)	9	1.4 (1.0)	5	0.01 (0.01)	5	0.0	16	0.0
2001	4	0.7 (0.5)	4	1.5 (0.6)	12	1.5 (0.8)	4	0.0	5	0.0	17	0.0
2002	4	0.2 (0.1)	4	1.7 (1.3)	9	1.4 (1.1)	4	0.0	5	0.0	14	0.0
2003	5	0.8 (0.3)	5	1.1 (0.9)	12	0.5 (0.6)	3	0.0	5	0.0	17	0.0
2004	-	-			26	2.1 (2.1)	-	-	-	-	58	0.0

Year	Below Mactaquac						Above Mactaquac					
	Hammond		Keswick		Nashwaak		Meduxnekeag		Shikatehawk		Tobique	
	# sites	Mean	# sites	Mean	# sites	Mean	# sites	Mean	# sites	Mean	# sites	Mean
2005	-	-			25	1.5 (1.2)	-	-	1	0.0	58	0.0
2006	-	-			26	0.9 (0.7)	-	-	-	-	57	0.0
2007	-	-			26	1.4 (1.0)	4	0.0	6	0.0	29	0.0
2008	-	-			16	1.3 (1.1)	4	0.0	7	0.0	28	0.0
2009	-	-			11	1.1 (0.8)	4	0.0	7	0.0	17	0.0
2010	-	-			10	1.1 (1.0)	4	0.0	5	0.0	18	0.0
2011	-	-			10	0.6 (0.4)	4	0.0	5	0.0	18	0.0
2012	-	-			10	1.7 (1.1)	-	-	-	-	16	0.0

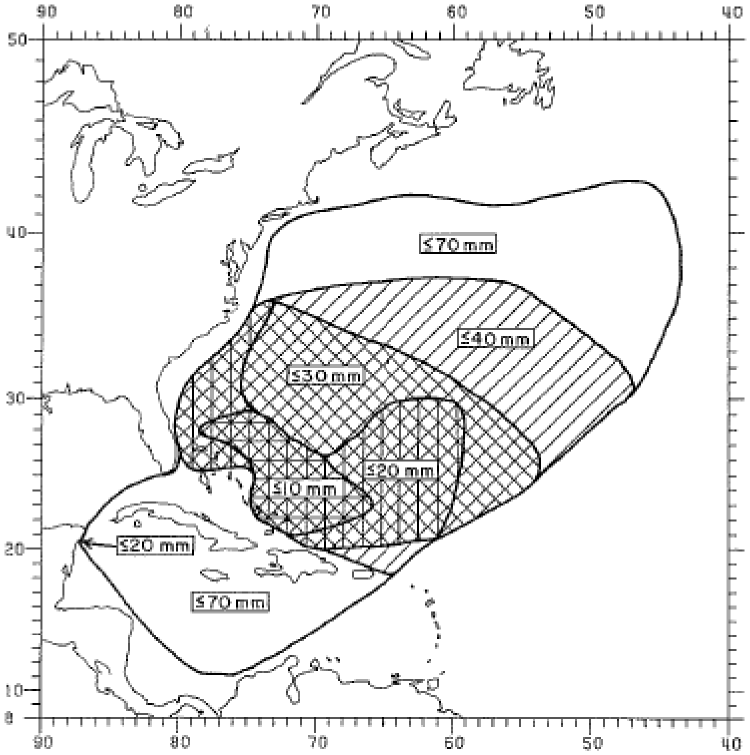

Figure 1.Spatial distribution of American eel leptocephali, by size (mm). Figure is from Kleckner and McCleave (1985).

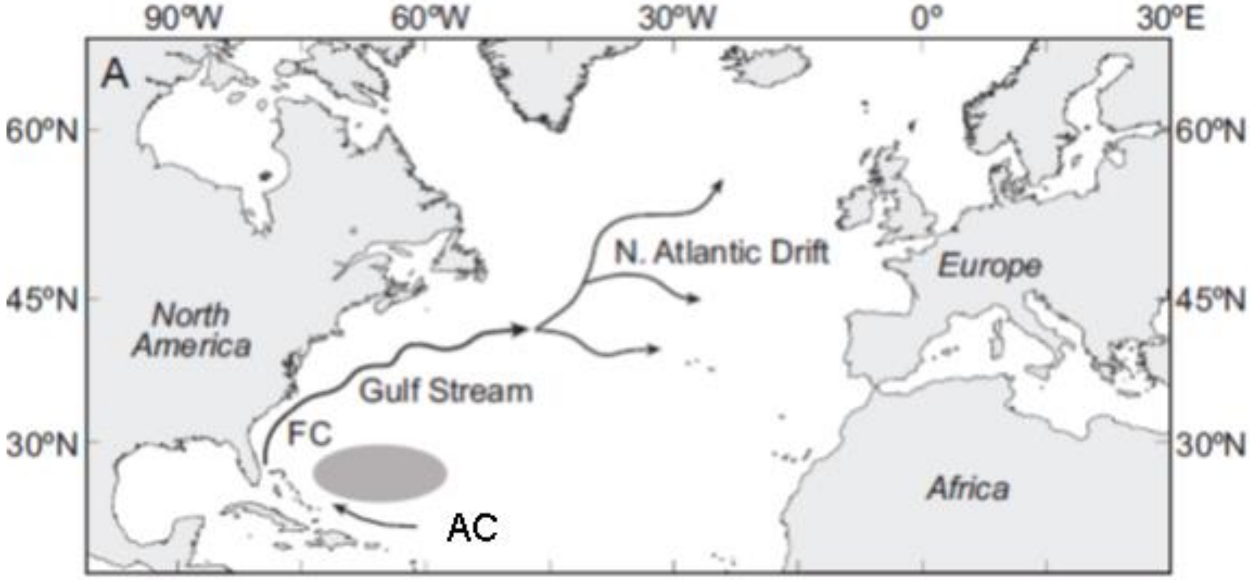

Figure 2. The presumed spawning area (gray shading) and main currents, including the Antilles Current (AC), Florida Current (FC) and the Gulf Stream, thought to be critical for leptocephali dispersal. Figure is modified from Miller et al. (2009).

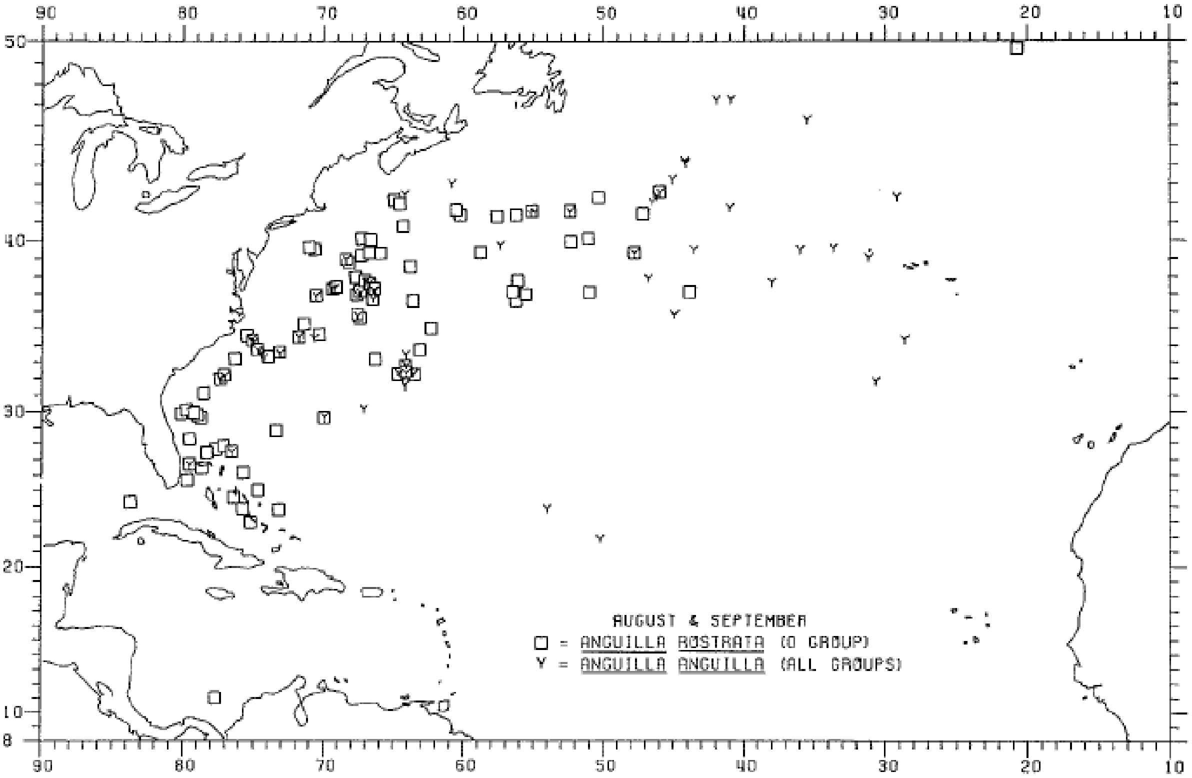

Figure 3. Distribution of American and European eel leptocephali in August and September. Figure is from Kleckner and McCleave (1985).

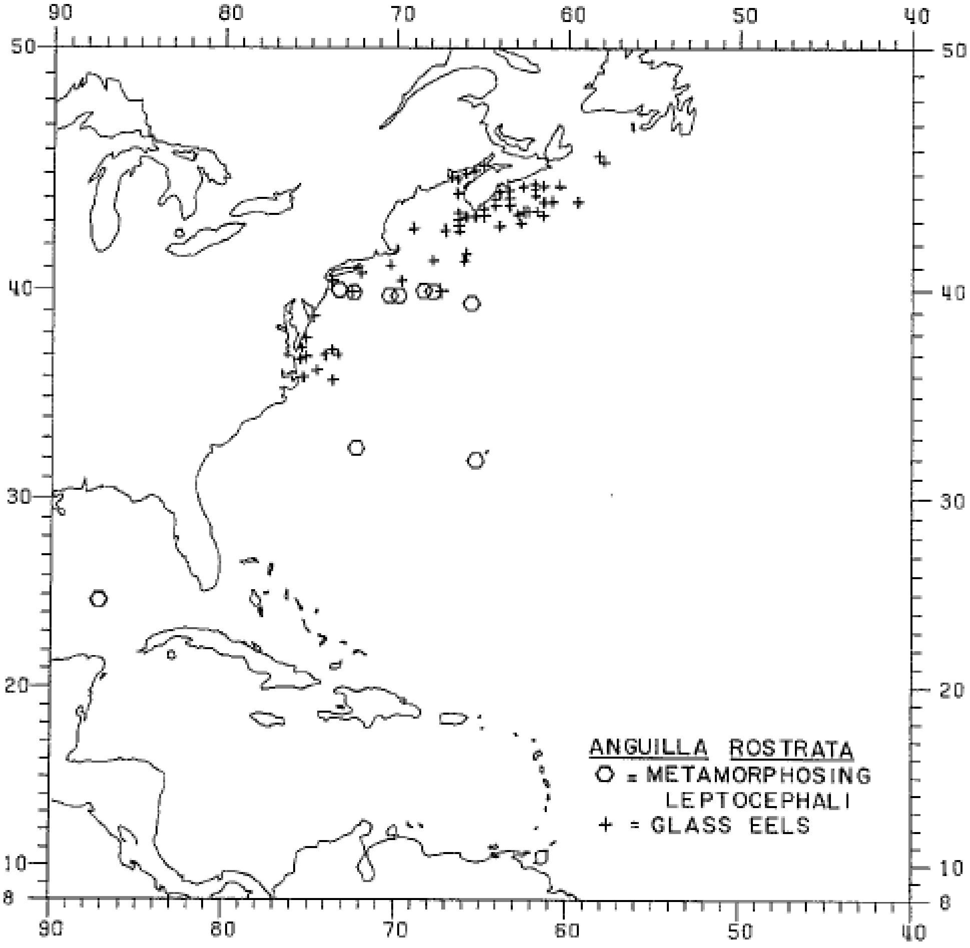

Figure 4. Distribution of glass eels from collections examined by Kleckner and McCleave (1985).

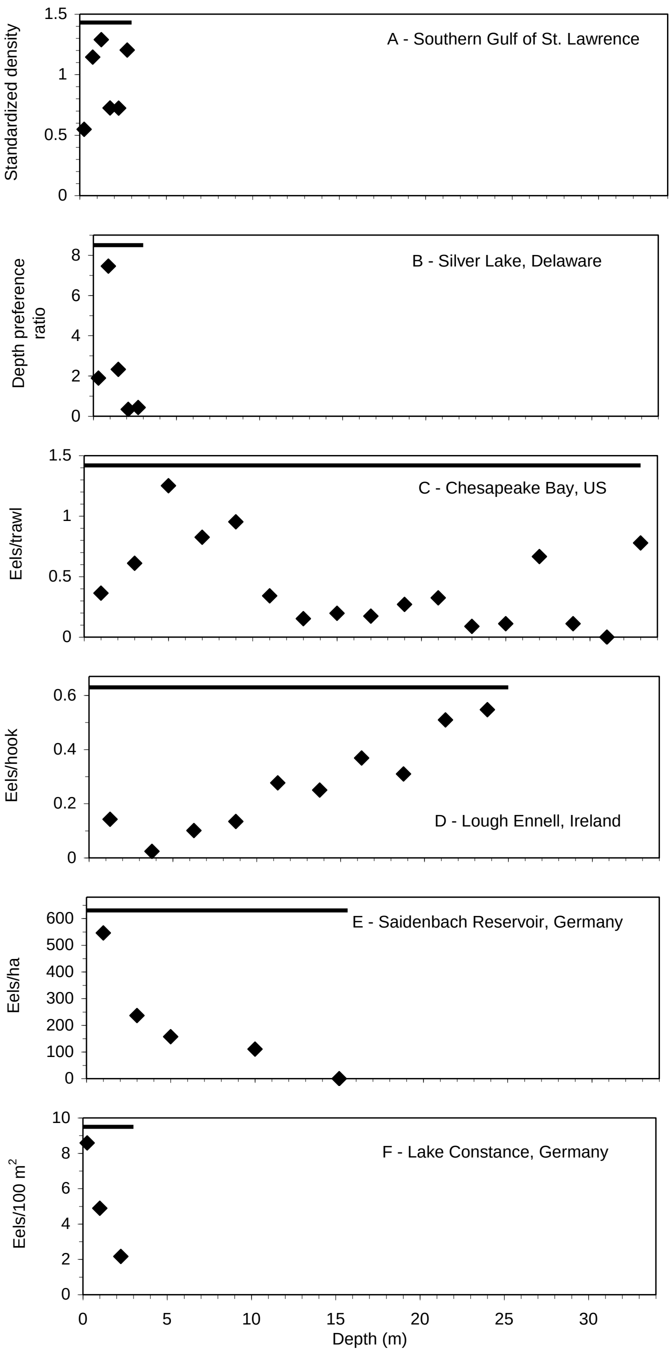

Figure 5. Abundance indicators of American and European eels vs. depth. Horizontal lines indicate the range of depths covered in each study. Panel A: densities from glass bottom boat surveys in the southern Gulf of St. Lawrence (J. Hallett, D. Cairns, and S. Courtenay, unpubl. data). Densities are standardized by dividing densities within depth ranges by mean densities in all depth ranges. Panel B: ratio of observed to expected counts from radio-tracking in Silver Lake, Delaware (Thomas 2006). Panel C: eels per trawl in Chesapeake Bay, US (Geer 2003). Panel D: eels per longline hook in Lough Ennell, Ireland (Yokouchi et al. 2009). Panle E: densities from diving surveys, Saidenbach Reservoir, Germany (Schulze et al. 2004). Panel F: mean densities across habitat types from electrofishing and trammel nets, Lake Constance, Germany (Fischer and Eckmann 1997). Figure is from Cairns et al. (2012).

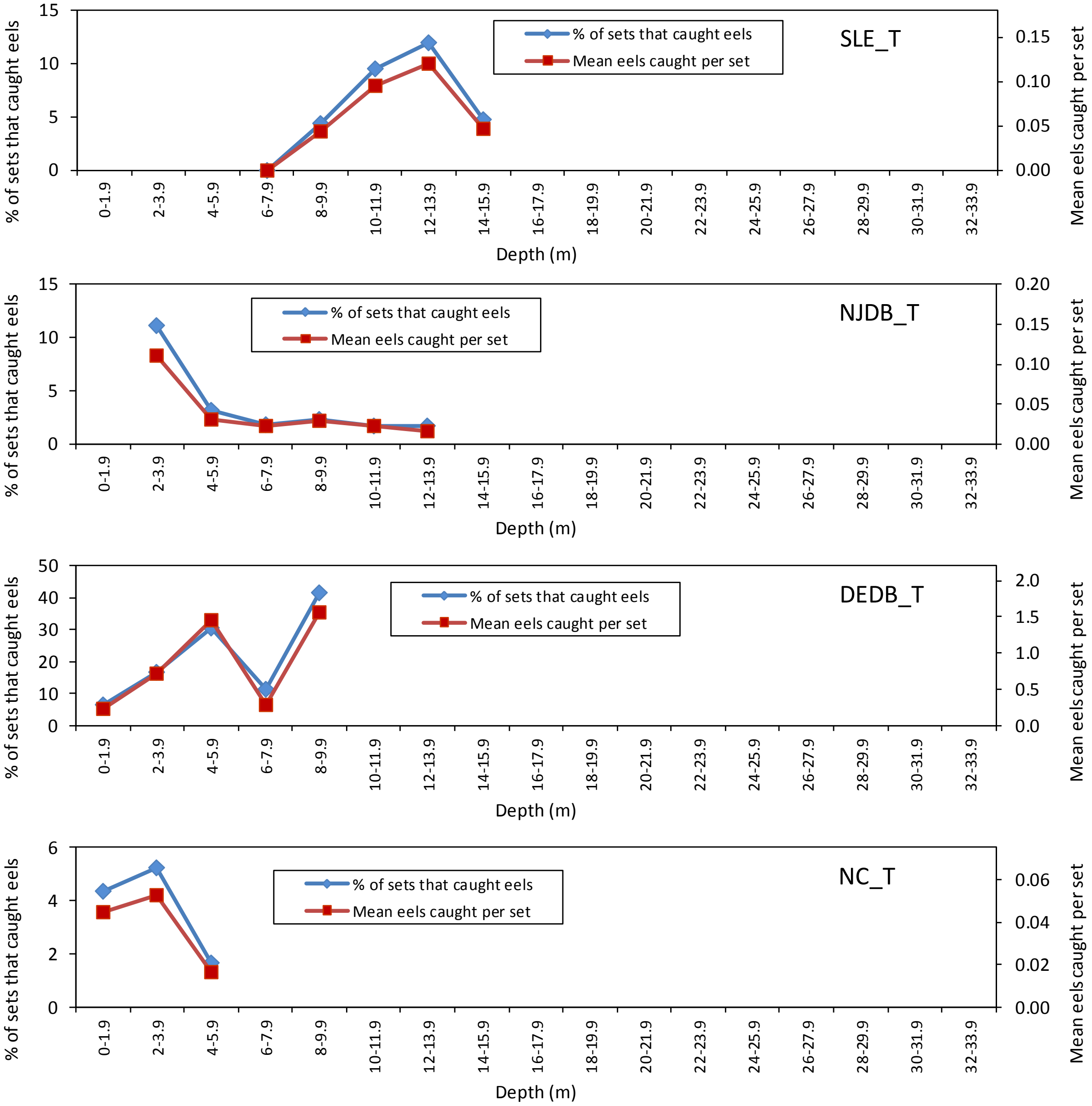

Figure 6. Percent of sets that caught eels and mean eels caught per set, by 2 m depth bins, in the SLE_T, NJDB_T, DEDB_T, and NC_T surveys. Figure is from Poirier and Cairns (unpublished manuscript, in prep.).

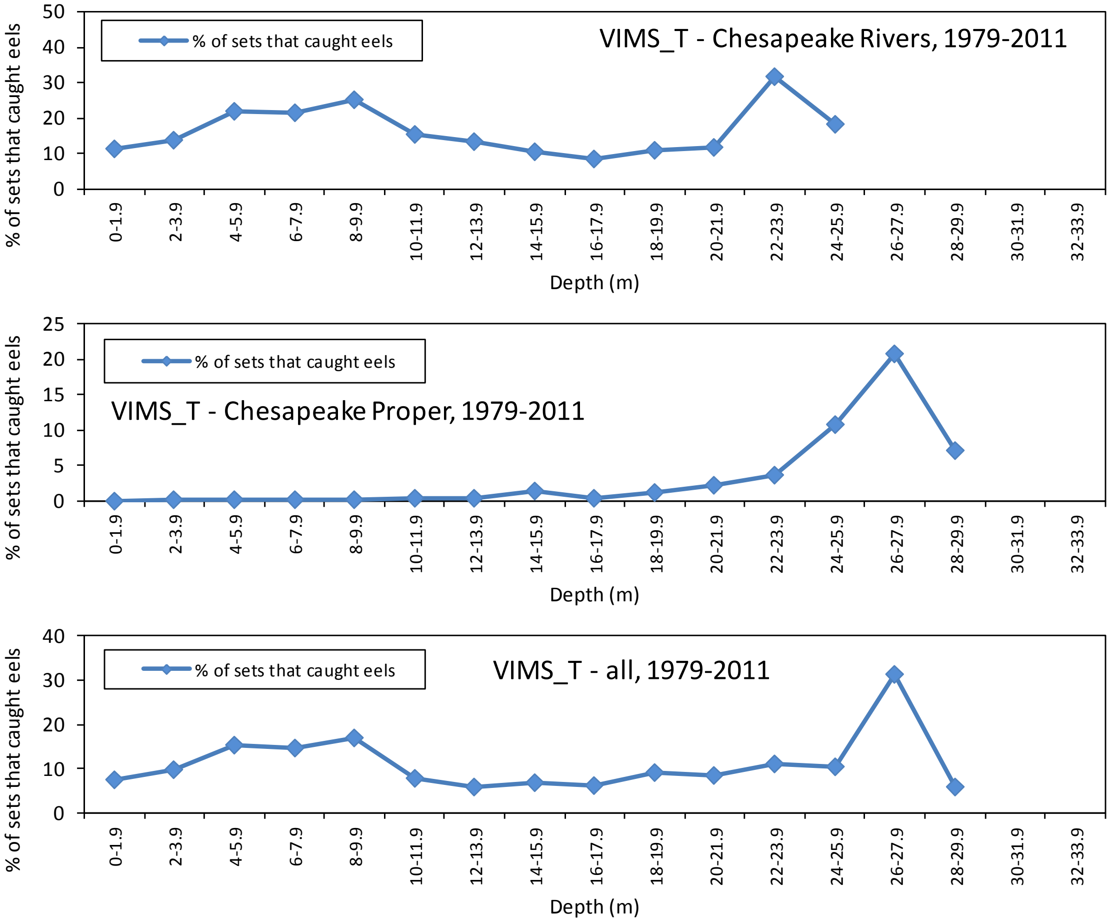

Figure 7. Percent of sets that caught eels, by 2 m depth bins, in rivers on the west side of Chesapeake Bay, in Chesapeake Bay proper, and in the full VIMS_T dataset. Figure is from Poirier and Cairns (unpublished manuscript, in prep.).

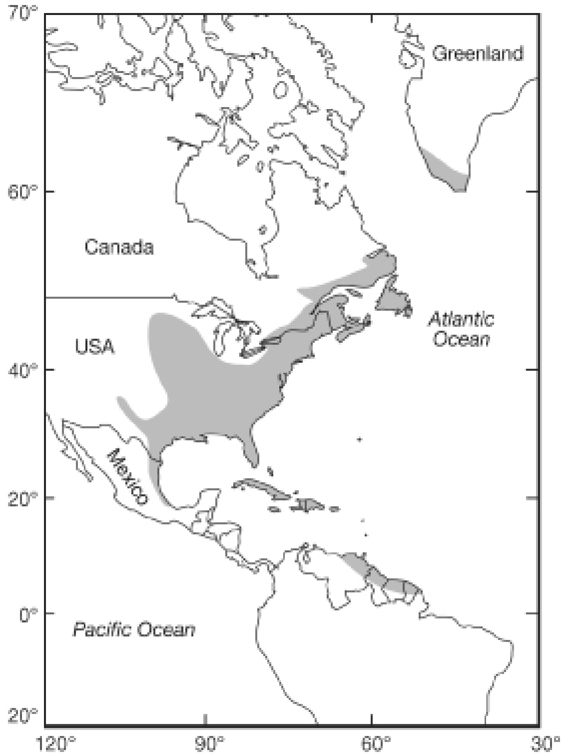

Figure 8. The geographic distribution of the American Eel in continental waters. Figure is from MacGregor et al. (2010).

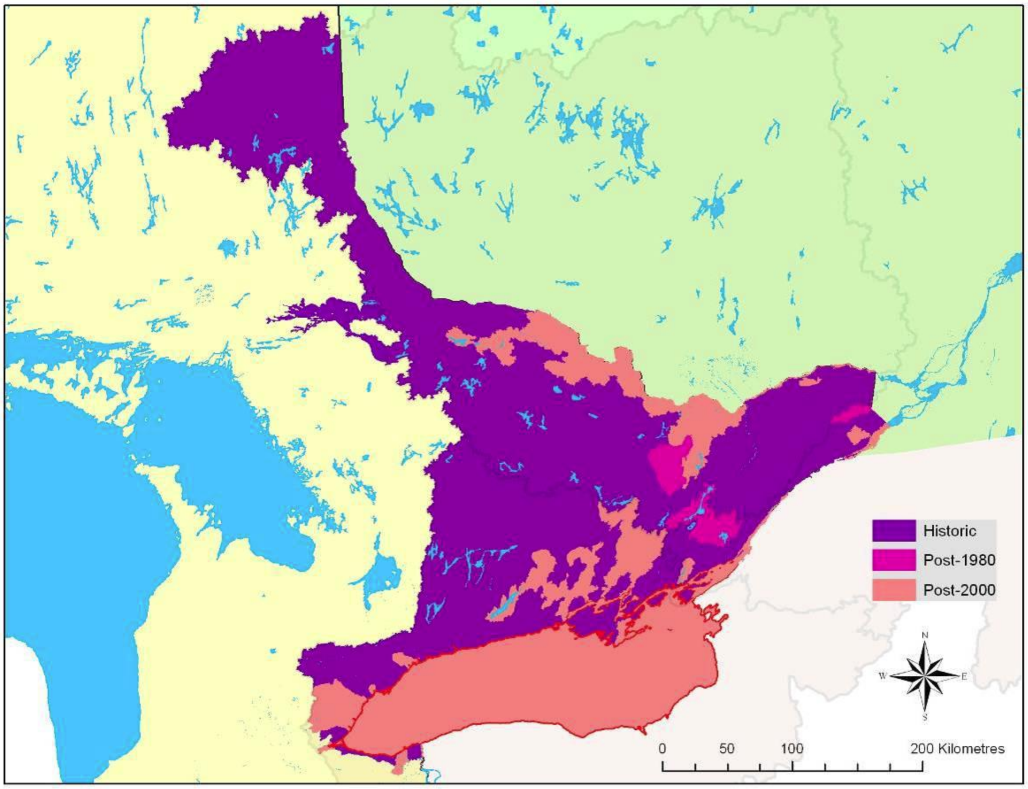

Figure 9. Contraction of the distribution of the American Eel in Ontario. Figure is from MacGregor et al. 2010.

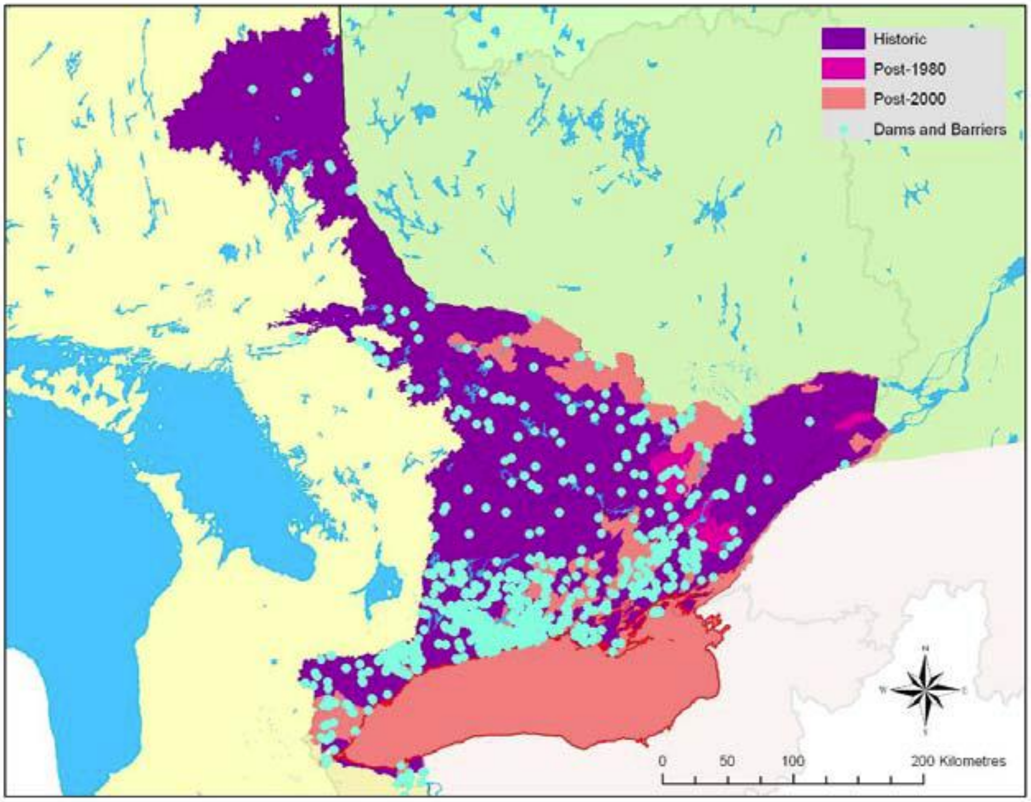

Figure 10. Location of dams, barriers, and other water control structures within the historical range of the American Eel in Ontario. Figure is from MacGregor et al. (2010).

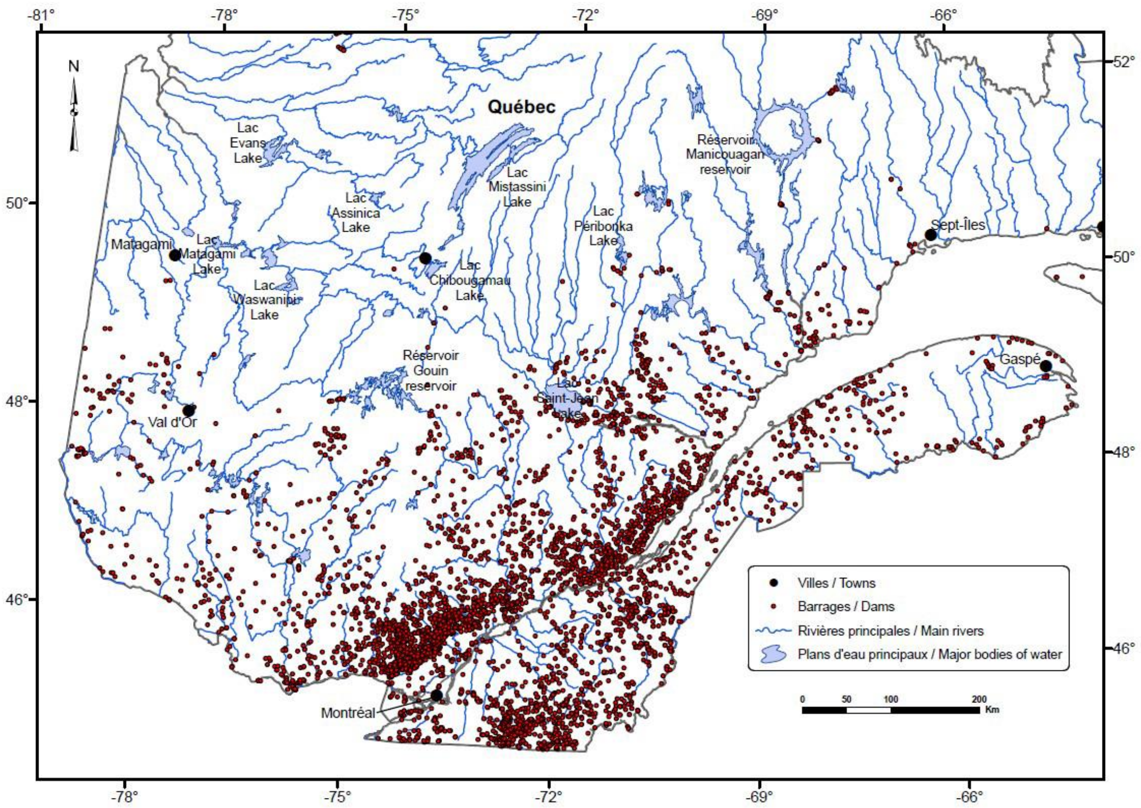

Figure 11. Dams identified in the Centre d'Expertise Hydrique du Québec (CEHQ) database (as of 27 January 2010). Figure is from Tremblay et al. 2011.

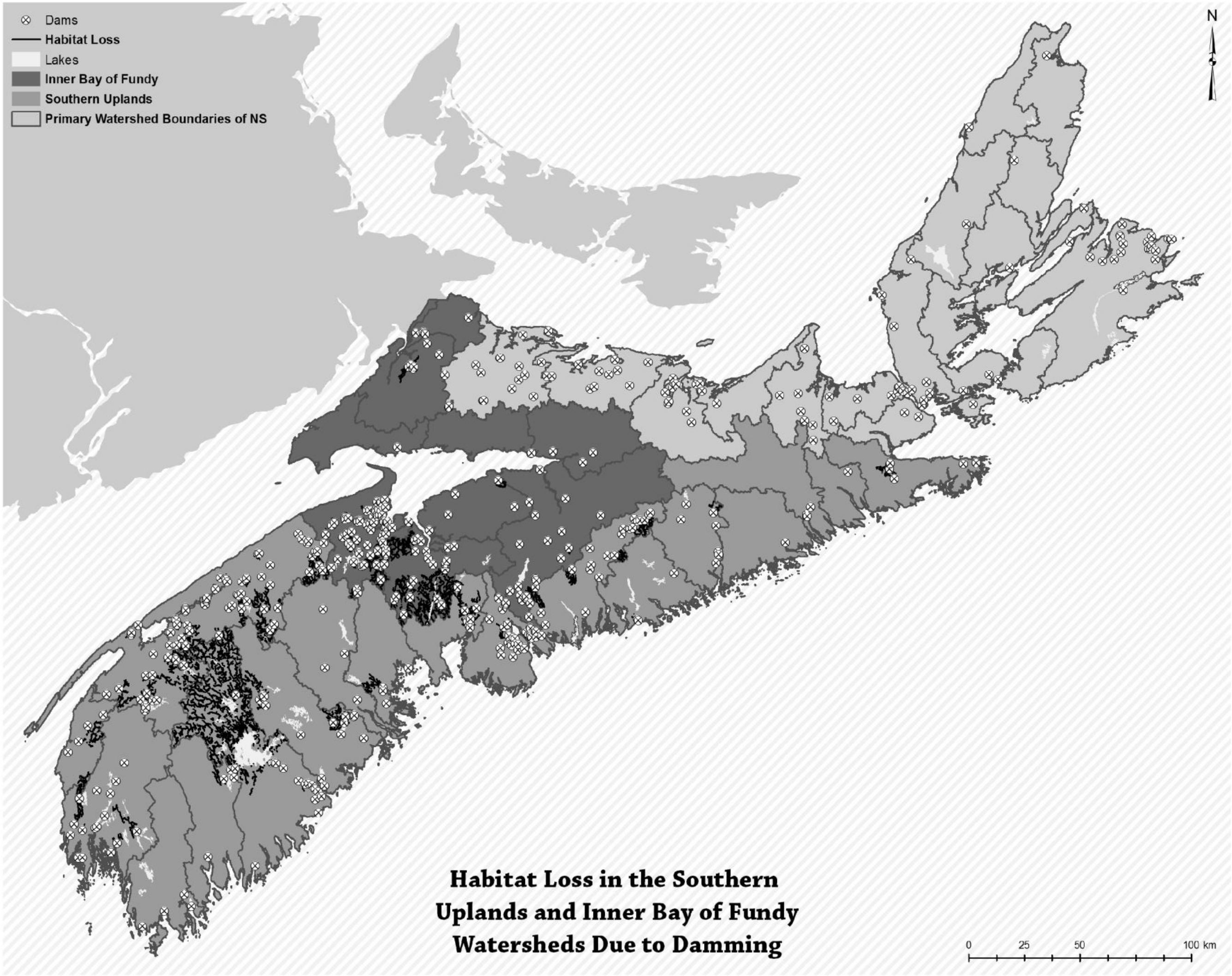

Figure 12. Barriers in Nova Scotia and habitat identified to be restricted to salmonids by dams in the Inner Bay of Fundy and the Southern Upland study areas. Figure is from Fielding (2011).

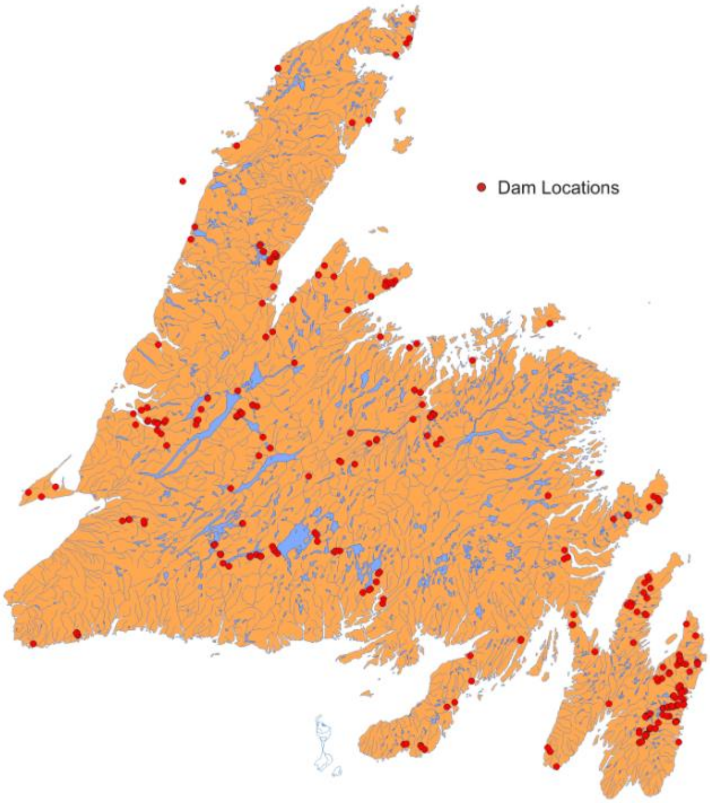

Figure 13. Barrier locations in insular Newfoundland. Figure is from Nicholls (2011).

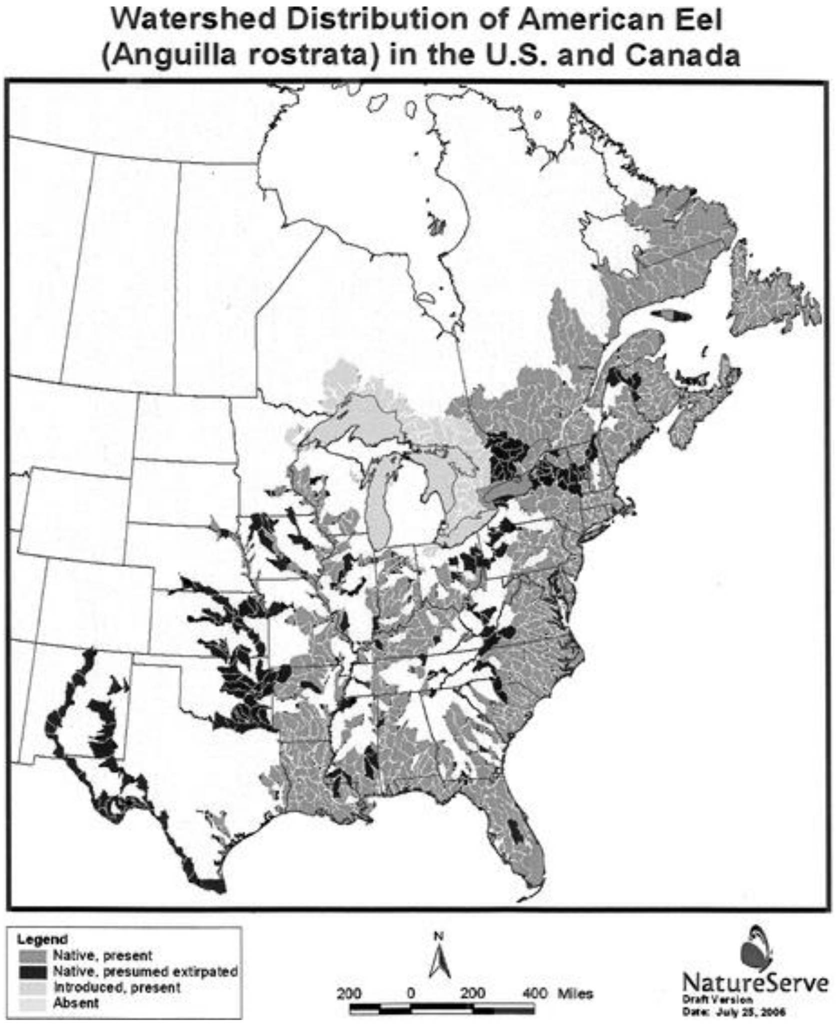

Figure 14. Current and historic distribution of the American Eel in the United States and Canada. Areas indicated in black shading are watersheds where eels are presumed to be extirpated. Image from Natureserve.