

Natural Heritage, Anthropogenic Impacts, and Biopolitical Issues Related to the Status and Sustainable Management of American Eel: A Retrospective Analysis and Management Perspective at the Population Level

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Abstract.—We examine historical, archaeological, and current patterns in American eel *Anguilla rostrata* use, abundance, and distribution to improve understanding of current population-level status. Our research indicates that distribution and abundance has changed significantly in response to the cumulative impacts of fishing, turbine mortality, and major loss of freshwater habitat. The 1950–1970 peaks in dam construction and turbine mortalities, together with the unprecedented North American harvests in the 1970s, have led to a perilous synergy of effects at the population level. Based on our findings, we call for coordinated conservation and management actions for American eel across North America. Preservation of life cycle diversity and coordinated conservation actions are required across the range to ensure continued and improved societal benefits, protect the legacy of cultural and natural heritage values, restore ecological services, and reinstate the benefits to biodiversity provided by this unique and important species. Finally, we describe key elements and recent progress in recovery planning.

Introduction

American eel *Anguilla rostrata*, once a widespread, abundant, and important species throughout all accessible freshwater and coastal habitats of eastern North America gradually has diminished in abundance and distribution over the past century, particularly in freshwater habitats. MacGregor et al. (2008) describe how the invisible collapse phenomenon (Post et al. 2002) applies to American eel, given its wide geographic range, diverse and localized fisheries, and paucity of coordinated management and stock assessment at the population level. In fact, eels appear to have declined or disappeared from many watersheds long before adequate records were kept. Consequently, biologists, particularly those new to the profession, often are surprised to learn that eels previously existed, were important, and were locally abundant in places like Lake Timiskaming in the upper Ottawa River watershed, northern Ontario. This loss of corporate memory, with respect to past abundance and distribution, has contributed to shifting baselines (Pauly 1995; Sáenz-Arroyo et al. 2005; Pinengar and Engelhard 2008) in our understanding of American eel status, leading to difficulties in implementing adequate conservation measures.

While now a species of concern in some jurisdictions (COSEWIC 2006; OMNR 2007), shifting baselines and perspectives on the status and importance of eels clearly influences the management attention and conservation priority they receive (MacGregor et al. 2008). For instance, similar to the connections between humans and Pacific salmon (Lackey et al. 2006a), indigenous peoples and European settlers experienced long and close associa-

tions with the American eel in freshwater. Like Pacific salmon, eels took on spiritual status with some people in eastern North America (Prosper and Paulette 2003) and were clearly important for sustenance and commerce in North America for centuries. In contrast to Pacific salmon, however, the earlier importance and abundance of eels appear to have been forgotten by the mid-1900s. By that time, eels were viewed by some fisheries managers as a direct loss of nutrients in freshwater systems and as competitors with trout and salmon, and they were certainly in disfavor with many anglers (Smith and Saunders 1955; Eales 1968). These perceptions have limited efforts to conserve and manage American eel on a sustainable basis during the 20th century.

Markets for American eel recently have grown substantially, and its commercial value has generated renewed attention. At the same time, government and societal interests in protecting and restoring biodiversity, ecological services, and natural heritage values have increased, sparking considerable attention on this highly unique and historically important species. Others view eels as a bellwether species sending an integrated message about the state of the environment (Prosper and Paulette 2003; Hoag 2007; Zettler 2007). These interests have led to growing concern over the condition of the American eel population (Casselmann 2003; Dekker et al. 2003; Commanda 2007; MacGregor et al. 2008).

Varying opinions regarding the status of American eel exist among the some 25 jurisdictions having responsibility for their management (ASMFC 2000, 2006; COSEWIC 2006; OMNR 2007; U.S. Office of the Federal Register 2007). Perceptions of eel status appear to be parochial in nature, depending in

part on the location of a jurisdiction in relation to resource use and distance from the common source of recruitment, the Sargasso Sea. Given conflicting opinions regarding the population-level status of American eel, we re-establish indications of former abundance and distribution across North America by means of a comprehensive synthesis and review of historical and archaeological information. After examining changes in American eel abundance, we summarize the need for conservation action and coordinated binational management.

American Eel Life Cycle and Related Management Complexities

The American eel is a long-lived (Casselman 2003), semelparous, highly migratory, and apparently panmictic species (Avisé et al. 1986; Wirth and Bernatchez 2003). Its complex life cycle is illustrated in Figure 1, and more detailed descriptions are available in Tesch (1977) and COSEWIC (2006). American eel are described as catadromous, but this life history strategy is facultative because some eels appear to spend their entire life cycle in marine or brackish environments (Lamson et al. 2006). Catadromy in anguillid eels apparently evolved from local migrations of tropical eels as a result of long-distance dispersal

of leptocephali from tropical spawning sites (Tsukamoto et al. 2002). Nevertheless, freshwater occupancy clearly has been an important part of their population-level life history strategy. Many eels, particularly at the extremities of their range in Ontario and Québec watersheds of the St. Lawrence River/Great Lakes basin, spend almost two decades in freshwater (Casselman 2003), and virtually all are females. Impacts on the freshwater contingent may be especially important as they affect predominantly highly fecund females.

Given the panmictic nature of the eel life history, anthropogenic impacts accumulate over a wide geographic range on one common spawning stock. Significant harvests occur at all continental life stages (MacGregor et al. 2008), and mortalities and habitat losses have been pronounced across the range. Anthropogenic stressors are widespread and cumulative across much of the North American range, having population-level effects that must be considered in management.

Historical Importance of American Eel to Early Indigenous Peoples and European Settlers

Baseline understanding of the American eel has eroded over the 20th century, as information and

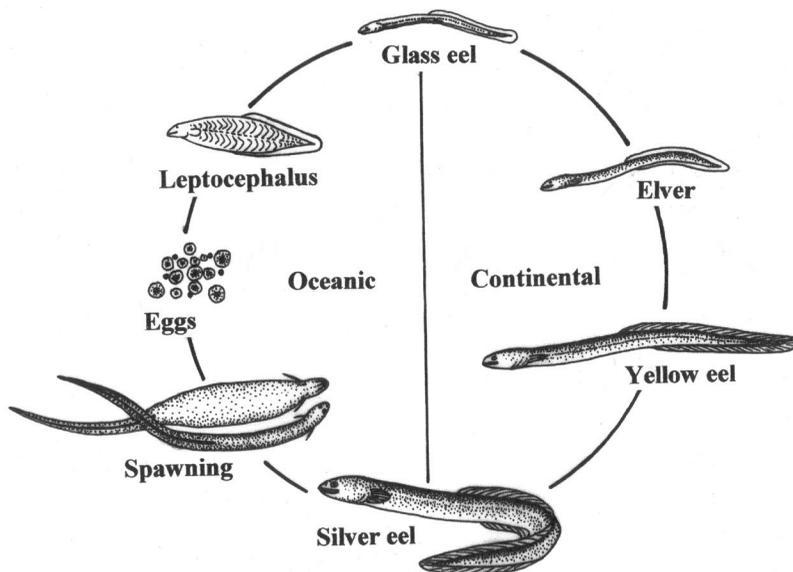


Figure 1.—American eel lifecycle.

knowledge have been lost or forgotten. Anecdotal information from an earlier time, and early eyewitness accounts gleaned from historical documents, archaeological records, and traditional ecological knowledge of indigenous peoples, provide valuable insight into the past distribution, abundance, and importance of American eel (Pauly 1995; Allen 2007a; Pinnegar and Englehard 2008). Here, we provide a comprehensive synthesis of such information for American eel, progressing through time to the 20th century.

Eels in Traditional Indigenous Lifeways

Eels have played a long and significant role in the lives of indigenous peoples in eastern North America. Junker-Anderson (1988) states that “most contemporary observers agree the eel was the single most important of the fish species for all of the Iroquoian peoples, with the possible exception of the Mohawks.” Eels also were important in traditional Algonquin territory (Allen 2007b, 2007c). In pre-contact and early contact times, eels were so abundant, widely dispersed, easy to catch at certain times of year, highly nutritious, and easy to preserve that they were considered as gifts of Manitou (or Manidoo, the Good Spirit).

Indigenous peoples in eastern North America had many names for American eel and place names for important fishing areas, and this information provides valuable clues in improving our understanding of past abundance and distribution. The Mi'kmaq people called them Kat. The Algonquin words pimizi (McGregor 1994) and Ojibwe bimizi (Baraga 1878), derived from Algonquin pimide (McGregor 1994) or Ojibway bimide (Baraga 1880) meaning greasy, emphasize the high-calorie, high-fat content of eel as food. The Seneca, south of Lake Ontario, called the eel goda:noh (Bardeau 2002). Swatara Creek in Swatara Township, Pennsylvania is named after an Iroquoian or Susquehannock term meaning “where we feed on eels” (Dohne 2004). An Indian village at the site of Sunbury, Pennsylvania on the Susquhanna River was originally called Schahamoki, “the place of the eels” (Heckewelder 1823). Franklin Hough describes a place on the Onondaga River called Ongontenayea or Aquegontenayea, meaning “a place remarkable for eels,” some 8 km downstream of the river outlet at Oneida Lake (Munsell 1861).

The Mi'kmaq had a deep connection with eels as a traditional and important food source (Prosper 2001; Prosper and Paulette 2002, 2003). Eels also were considered to have many spiritual qualities and to be a spiritual being; they were used as a ceremonial offering and found their place in traditional stories. Eels were offered in a ceremony called Apuknajit, feeding of the Grandfather (Marshall 1997), to give thanks to the spirits for allowing the people to survive through the most difficult time of the year. Seventeenth-century accounts indicate that “if they had roasted an Eel, they also believed that this would prevent them from catching [one] at a different time” (Denys 1672:480) and that frightened people threw eels on the fire to appease the devil (Thwaites 1896–1901). Such taboos indicate spiritual connections with eels. This spiritual connection continues today as evidenced by a 2007 letter to Fisheries and Oceans Canada by Elder Dr. William Commanda, Algonquin spiritual leader, in which he wrote,

I am raising my voice concerning the plight of American eel. The eel has been of spiritual, nutritional and material importance to the Indigenous Peoples of the eastern seaboard, and to my ancestors of the Ottawa River Watershed, since time immemorial...I believe the eel spirit is intrinsic to the sacred Seven Fires Prophecy Wampum Belt that I have carried for the people for thirty six years. It is this prophecy that tells us that humanity is now at a cross roads, and that we need to regenerate our relationship with Mother Earth and each other. (Commanda 2007)

Indigenous peoples established close connections with eels in the St. Lawrence River, Lake Ontario, and Ottawa River watersheds. Before timber harvesting, in areas such as the Madawaska River watershed in Ontario, eel harvesting was part of an efficient food procurement process involving farming, fishing, hunting, and collecting (Allen 2004, 2007d). Le Jeune's 1634 description (Thwaites 1896–1901) notes the Montagnais' reliance on eels from the St. Lawrence River and describes fishing techniques and preparation of eels. Father Louis Hennepin wrote that “the most considerable fishery...is that of the eels, which are very large” (Hennepin in Thwaites 1903:2:524). Fresh eels were the primary food

during September and October. Eels were dried when they were abundant, providing sustenance from November through January. Smoked eels, being lightweight and highly nutritious (Casselman 2003), were commonly used as traveling food (Junker-Anderson 1988). Indigenous peoples often gave eels as gifts to early European travelers or used them in trade (Beauchamp 1916).

Twenty-one Ontario archaeological sites within the Lake Ontario–St. Lawrence River watershed yielded eel remains of precontact age between 500 and 1,000 years old (Pearce 1977; Junker-Anderson 1988; Fitzgerald 1990; Reed 1993; Finlayson 1998). In addition, two archaeological sites more than 4,000 years old on the Québec side of the Ottawa River yielded substantial eel remains (Clermont and Chapdelaine 1998; Clermont 1999; Clermont et al. 2003), and a complex of stone weirs and pools was documented in 2007 in Rapides des Allumettes (BkGg-29¹) (W. A. Allen, Heritage One, unpublished data). At Pointe-du-Buisson Archaeological Park, near Montréal, two sites yielded eel bones dating from 920 to 940 A.D. (Courtemanche 2003) and 500–1000 A.D. in a second case (Cossette 1995). Aborigines harvested eels as recently as the early 20th century within the upper Ottawa River watershed in Ontario's Mattawa and Montréal rivers (Allen, unpublished data).

In Virginia, traditional homeland of the Virginia Algonquins (Feest 1978), American eel remains were documented at several sites predating the arrival of Europeans (Whyte 1988, 2001, 2002; Whyte and Thompson 1989; Egloff et al. 1994; Clark et al. 2005). Some artifacts at a site in Delaware tested positively for American eel protein residues (Puseman and Cummings 2004). In New York State at the Bates site in Chenango County, a site carbon-dated to 1190 A.D. yielded eel remains (Ritchie and Funk 1973).

Indigenous peoples fished eels by using specialized eel splint baskets, weirs, and spears, particularly at night. Le Jeune described

certain ones who will take three hundred in one night...After being well smoked, they are piled together in large packages,

about a hundred in each. Here you have food up to the season of the snow, which brings them the Moose. (Thwaites 1896–1901:6:311–313)

De Quen noted that “eels are so abundant [at Onondaga] in the summer that a single fisherman can harpoon as many as a thousand in one night” (Thwaites 1896–1901:42:97). Father Louis Hennepin (Thwaites 1903:2:524) described the Iroquoians spearing an “infinite number” of eels by the light of a birch bark torch at night, being particularly successful because the “great white porpoises which pursue them make them fly towards the banks of the river where porpoises cannot follow.”

Early explorers and missionaries described weirs as important eel fishing methods of indigenous peoples (Charlevoix 1761; Beauchamp 1916). The Jesuit Relation of 1634 describes the construction of weirs “capable of holding five or six hundred eels” (Thwaites 1896–1901:6:309). Stones were extended out at the sides to guide eels into a trap. A weir historically used by Mi'kmaq to trap eels on the Mersey River, Nova Scotia is estimated to be 4,000 years old (Prosper and Paulette 2002). In fall on the Delaware River, the Lenape would catch thousands of downstream migrants in a single night, using a kind of basket weir or eel pot (Wade 2007). Archaeological study has been undertaken at several stone weirs that have a unique downstream “V” suggesting the ancient capture of downstream-migrating mature eels. These weirs include the 2,500-year-old Satucket River weir in Massachusetts (Watts and Watts 2004), 11 weirs on the Passaic River in New Jersey (Lutins 1992; Lutins and DeCondo 1999), and the Otselic River Weir in New York (E. McDowell-Loudan, State University of New York College at Cortland, personal communication) on a tributary of the Susquehanna River where remnants of more stone weirs are still visible in low water (Dohne 2004). In addition, sharpened wooden stakes in Maine's Sebasticook Lake fish weir in the Kennebec River watershed, where eels were abundant, have been dated to between 5,800 and 1,700 years old (Miller et al. 2006).

Indigenous peoples used eels in multipurpose material and medicinal fashions. The Mi'kmaq used eel skins as wrist and ankle straps to provide support and relief from rheumatism. Eel skins (kadaagel) were used as braces and bandages: “juniper balsam and eel skin make a good poultice for sprains” (Lacey

¹ This paper uses the standard “Borden” numbering system used across Canada at registered archaeological sites (see Garard 1967).

1977; Prosper 2001) and to set broken bones (Allen, unpublished data). In New York, eel oil was collected by parboiling and was used to relieve ear aches (Allen, unpublished data). Eel skins also were used as hair braids; Champlain described indigenous girls attending dances “with a tuft of their hair behind tied up with eel skin which they arrange to serve as a band” (Champlain Society 1922–1936:4:312). Eel skins were used as bindings for sleds, moccasins, and clothing and for tying spears and harpoons on sticks (Prosper and Paulette 2003) since they tighten when dried. In Ontario, eel skins were used as bow grips, and fatty eel flesh was used to waterproof clothing (Allen, unpublished data).

In the United States, at least three of the New York State six nations—the Cayuga, Onondaga, and Tuscarora—had, at one time or another, an eel clan (Morgan 1877). Clans named after fish are rare so eel clan designations are a further indicator of the significance of this species (Casselman 2003). Tooker (1978) documented three of 14 Onondaga titles that indicated eel clans. Before 1800, the Mahican had a yellow eel clan (Barton 1797). In Indiana, in the upper Mississippi watershed within traditional eel range, an entire book has been written about the Eel River Tribe, a Wabash confederacy (Floyd 2007). Indigenous surnames include Chief Swimming Eel (Speck 1940) among the Scaghticoke on the New York/Connecticut border and Chief Eels from the Kawartha Lakes area of Ontario (Guillet 1957).

As Europeans moved west, many indigenous peoples moved outside the traditional native range of eels to the Lake Erie watershed where eel clan significance, over a few generations, appears to have dissolved into subclans. Nevertheless, indigenous peoples have maintained their connection with eels in many areas of Canada (Prosper 2001). While eel weirs have long been banned in many areas (Canada 1868a; Fraser 1912; Pulla 2003), indigenous peoples in the Maritimes region have continued their practice of spearing eels during both open water seasons and ice-covered periods. However, there is concern that as eels decline in abundance, the close connection and tradition associated with eels soon will be lost (Prosper 2001).

Importance of Eels to European Settlers

When European settlers arrived in North America, they did not keep harvest records, but historical

anecdotes survive. For instance, Father Francois du Creux (1664) suggests “an almost unlimited supply” of eels. An account from 1652 to 1653 at Trois-Rivières notes that “the eel constitutes a manna exceeding all belief” (Thwaites 1896–1901:40:215–217); “a wonderful manna for this country, and one that costs nothing beyond the catching” (Thwaites 1896–1901:45:193). The eels kept well and were considered tastier than those in France because they swam in the vast waters of the St. Lawrence River rather than their muddy environments in France.

In the 1800s, eels of large size and fine quality were taken everywhere within the Gulf of St. Lawrence: “They are in reality a very valuable description of fish; they are very numerous, very prolific... They are in great esteem for the table, and the consumption in our large cities is considerable” (Canadian Naturalist and Geologist 1859:98). In the late 1800s, the lower St. Lawrence River eel fisheries were considered to be the most productive in the world, and their quality unsurpassed (The New York Times 1880a). Here, they deployed weirs, catching eels during tidal events in September and October; one weir was reported to have taken 3,000 eels at a single tide, but an average good catch in the late 1800s was considered to be 1,000–1,500 eels. In 1870, 100,000 eels were reported to have been taken at the mouth of Rivière Ouelle. Farmers and other individuals along the St. Lawrence harvested eels by spears, usually at low tide, often making as much profit as the profit derived from farming the land (The New York Times 1880a).

Early settlers harvested large quantities of eels in weirs well upstream on the west branch of the Delaware River at Schewakhawken (now Sunbury, Pennsylvania) (Heckewelder 1823; Munsell 1880). “Prodigious” quantities of eels were taken by weirs and hurdles in the St. Lawrence River “from Québec, as high as Trois Rivières...[where] eels come down from Lake Ontario...great quantities are taken during the time this fishery lasts, they are salted and barreled up like herrings” (Charlevoix 1761:1:261–262). Eels were in such large quantity that they were easily caught and stored at little expense and hence were important as a staple food item for the poor (Charlevoix 1761:1: 228).

The Canadian Sessional Papers document many thousands of barrels of eels harvested commercially in areas extending from Ontario to the Atlantic provinces. Many were pickled for export to

Europe or taken in “barges filled with eels” to New York City (The New York Times 1936), but significant quantities apparently were sold fresh locally. The 1880s Sessional Papers indicate many concerns over declines in other species, whereas eels remained abundant and eel fisheries were productive throughout Québec and the Maritime provinces.

The implementation of regulations can indicate conservation concern over fish stocks. However, few conservation concerns over eel status were raised in the early years, and regulations that were implemented regarding eel fisheries were related largely to minimizing conflicts with other fisheries. Charlevoix (1761:1:228) described early conflicts as a “great outcry” over “porpoise” fisheries below Québec City interfering with eel fisheries: “for the porpoises having finding themselves disturbed...have retired elsewhere, and the eels no longer finding those large fishes in their way, swim down the river without any hindrance.” Hence, the success of eel fisheries was considered to be greatly reduced by the “porpoise” fishery. The Province of Prince Edward Island had fisheries legislation in existence as early as 1780: “An Act to regulate the Salmon, Salmon-trout and Eel fishery” (Prince Edward Island 1773–1834:1780). The then colony’s conservation concerns appeared to focus on salmon and on resolving conflicts among the various fisheries. A report of a fishery overseer in Lower Canada in 1823, perhaps concerned with eel conservation, commented on a localized issue concerning the use of spears, torches, and sticks by indigenous people to kill eels (Canada 1823). However, this issue may have been as much an indication of conflict among users as a conservation issue.

Many of the Canadian eel fisheries regulatory measures introduced in the late 19th century seem to have focused not so much on eel conservation but in dealing with access and allocation conflicts in the face of abundance declines of more valuable species. The Fisheries Act (Canada 1886) included prohibitions on the obstruction of streams by fishing gear, but added, “provided that the use of weirs for catching eels exclusively, and the use of mill-dams for catching eels, shall be prevented only in the case where, and at times when they injure other fisheries, or by completely barring any passage, they deprive other weirs of a share in the run of eels.”

Concerns were raised about eel fishing methods interfering with other fisheries, with spawning of other species (Canada 1868b), and about fishing for

other species under the guise of fishing for eels. The Province of Prince Edward Island enacted a regulation to prevent fishing for eels from boats by means of torches during October, November, and December (Canada 1893), but the regulation was really related to effects on other fisheries, not specifically to eel conservation. In Nova Scotia, concerns were raised with eel fishing practices destroying young alewife *Alosa pseudoharengus*, and a regulation was implemented to limit certain eel fishing practices at the mouths of streams between July and November was instituted (Canada 1889a). In Upper Canada (now Ontario), on the Trent River (a tributary of Lake Ontario), an 1817 report to the colony’s House of Assembly stated that “some unprincipled characters... [are] at full liberty to pursue their depredations by making weirs and dams across the river under the pretence of catching eels and whitefish, and do almost totally obstruct the passage of salmon up the same...and thereby cut off a very material source of supply to the back settlers” (Fraser 1912).

Similar conflicts occurred in the United States. For instance, the presidents of the Pennsylvania Commissioners of Fisheries and New York Fisheries, Game and Forest Commission agreed in 1895 that the eel weirs in the upper Delaware River “had to go” because many game fish were being caught that were stocked by Pennsylvania at “heavy expense” (The New York Times 1895), and concerns were raised over eel weirs illegally catching Atlantic salmon *Salmo salar* on the Beaverkill in Delaware County (The New York Times 1896). Conflicts with eel fisheries persisted at the turn of the century; while Pennsylvania had prohibited the use of eel weirs in the state, New York and New Jersey fishermen continued to take “wagonloads” from the Delaware River where eel weirs were still permitted (The New York Times 1901).

Early Commercial Harvests

Indigenous peoples used eels for trade, barter, and income (Supreme Court of Canada 1999). For instance, in the early 1620s, Champlain reported the indigenous peoples to be hard bargainers in trade; his hungry men gave their coats and other possessions for eels and that he acquired 1,200 eels at the rate of 10 eels for one new beaver pelt (Champlain Society: 1922–1936). Specialized eel spears were included in a 1684 French inventory at Fort Frontenac

(Kingston, Ontario) (Preston 1958), and trade in eels was reported as early as 1770 (Schmalz 1991:96).

In the early 1800s, eel harvests generally were not recorded, but it is clear that eels were “taken in great numbers in Lake Ontario and the rivers Niagara and St. Lawrence” (Talbot 1824). During the mid-1800s to 1900, commercial harvest records began to be reported in Canada’s Sessional Papers. At that time, eel prices (C\$0.11–0.13/kg) were not as high as Atlantic salmon in Québec and the Atlantic provinces (\$0.33–0.44/kg fresh) or as Ontario lake trout *Salvelinus namaycush* (\$0.22/kg) and lake whitefish *Coregonus clupeaformis* (\$0.18/kg). Although the quantities harvested commercially were quite small in comparison with other large fisheries, eels were always a valued commodity, in part because they were harvested regularly for sustenance. Quantities harvested by indigenous peoples and early European settlers for local uses were not reported, but clearly, eels were fished consistently by indigenous peoples for thousands of years and by early European settlers since contact. Indeed, eel fisheries were “highly productive, and enable[d] people to live when all else fails” (Thwaites 1896–1901:40:11–12).

Early commercial harvest records provide some insight into patterns of use and development of commercial eel fisheries. Ontario commercial eel landings were first reported in 1884 (Canada 1885) for Lake Ontario, the St. Lawrence River, and their watersheds. Ontario commercial eel fishing appears to have developed first in smaller tributary watersheds, likely as an extension of subsistence fishing practices. It is now clear that locally important eel harvests occurred in the inland waters of Ontario, particularly in the Ottawa and Trent River systems (Canada 1895, 1896, 1889b).

Harvest records in Canada’s Sessional Papers, spanning the late 1800s to 1900s, indicate that eels remained abundant and widely dispersed. Eel fisheries were locally important, providing stable exports and supplying local markets and family food. Eel fishing used relatively inexpensive techniques, including brush hurdles, weirs, spears, and pots. After a brief period in the early 1900s when eel prices rose to range from \$0.13 to \$0.20/kg and harvests in Ontario increased (Casselman 2003), harvests dropped to relatively low levels throughout most of Canada while prices fell by some 30% (Eales 1968) until the 1960s.

Twentieth Century Commercial Eel Harvests

Harvest data indicate that eels were abundant along the East Coast and in watersheds of North America at the beginning of the 20th century through to the mid-1900s, often accounting for more than 50% of total fish biomass (Smith and Saunders 1955; Ogden 1970; Lary et al. 1998). Trends in eel harvests for much of this period are described in detail by Eales (1968) and Casselman (2003).

Although long-term fisheries-independent data are lacking across much of the North American range, there is strong evidence of declining abundance (Haro et al. 2000; Casselman 2003; Dekker et al. 2003; Cairns and Casselman 2004; COSEWIC 2006; MacGregor et al. 2008). Early declines began in the Mississippi watershed where diminishing harvests were reported across 10 states between 1899 and 1922 (Coker 1929). In Canada, even into the mid-20th century, eels were considered to be underutilized (Eales 1968). However, harvests began to increase substantially after the 1950s. Total North American harvests rose from an average of 1,215 metric tons (mt) between 1950 and 1955 to an unprecedented peak of 2,915 mt in 1978 (Casselman and Marcogliese 2007). Lucrative glass eel fisheries also developed in North America at this time (Jessop 1987; ASMFC 2000). By the early 1990s, North American harvests had begun to plummet, and by 2004, eel harvests had declined to 840.4 mt. This decline occurred despite sustained high prices, well above the long-term mean (Casselman and Marcogliese 2007).

While there are temporal differences across regions in the onset of major declines in catches, overall trends in Ontario commercial harvests parallel those of Canada and the United States (Figures 2A–C). Between 1950 and 2003, Ontario commercial eel harvests averaged 80.1 mt (Figure 2A) but rose substantially in the 1970s to an unprecedented 228.2 mt. This harvest constituted 20% of total Canadian landings in that year. At the same time, North American harvests also increased dramatically in response to high prices and strong markets (Casselman and Marcogliese 2007), and concern grew over their sustainability (Kolenosky and Hendry 1982). In 1980, an experimental quota of 270 mt was implemented for Ontario’s

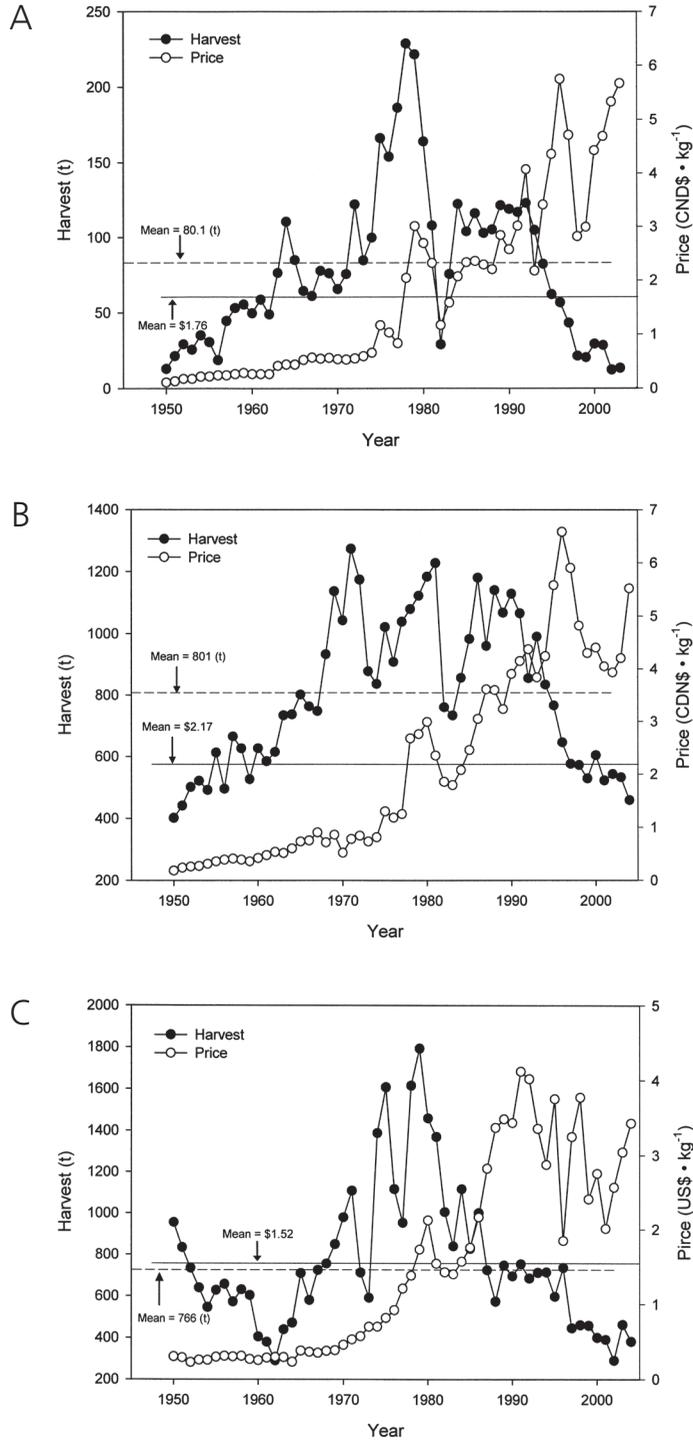


Figure 2.—Commercial eel harvest (metric tons) (solid circles) and weighted mean annual price/kg (Canadian dollars) (open circles) for (A) Ontario, 1950–2003; (B) Canada, 1950–2004; and (C) United States, 1950–2004. Mean harvest (metric tons) (broken line) and price/kg (solid line) are indicated. Ontario eel fishery was closed in 2004. Assembled from data from Casselman and Marcogliese (2007).

portion of the upper St. Lawrence River–Lake Ontario (USLR–LO; Kolenosky and Hendry 1982); this was a quota that was set when harvests were at record-high levels and was never approached. Ontario harvests declined substantially thereafter, in synchrony with strong harvest declines across North America (Figures 2A–C), as did the important silver eel harvests in Québec. Ontario fisheries-independent indices paralleled these trends (Casselman 2003). These declines, together with the dramatic reductions in recruitment to Lake Ontario, led to more widespread concern over the general status of American eel (Castonguay et al. 1994; ASMFC 2000; Casselman 2003). By the early 2000s, there were numerous calls for action (Casselman 2003; Dekker 2003; Dekker et al. 2003), and by 2004, the Ontario commercial fishery was closed.

Although effort data for commercial harvest statistics are universally lacking, if harvest and price are integrated across a broad geographic range, commercial catch data can be useful in detecting population-level shifts in abundance (Casselman and Marcogliese 2007). Prices during the early 20th century were low but began to rise in the late 1960s, particularly in the Atlantic provinces of Canada and some Atlantic coastal states (Casselman and Marcogliese 2007). By the late 1970s, both price and harvest had increased in Ontario and throughout Canada and the United States (Figures 2A–C), reflecting market demand from Europe and Asia (Loftus 1982; Casselman and Marcogliese 2007).

At that time, the American eel became the most valuable commercial fish species in Lake Ontario. However, despite sustained high prices in the latter half of the 20th century (well above the long-term mean), landings declined substantially, not only in Ontario, but throughout Canada and the United States (Figures 2A–C; Casselman and Marcogliese 2007).

Numerous issues may confound examination of trends in eel catches, depending on the density-dependent patterns of eel dispersal, geographic source of the data, and proximity to source of recruitment. Eels in the USLR/LO are at the extremity of the range. Edeline et al. (2007) describe density-dependent dispersal in juvenile European eel *Anguilla anguilla*, and it is probable that similar processes occur for American eel. If we assume that recruitment to the USLR/LO is density-dependent, as proposed by Casselman (2003), then changes

in abundance at the range extremities would reflect population-level changes. Assuming panmixia and that recruitment to Ontario is influenced by density (Casselman 2003), and noting that Ontario and North American harvests are synchronous, Ontario eel indices broadly reflect overall species abundance in North America. The longest index of recruitment is from Ontario's eel ladder at the Moses-Saunders Dam on the St. Lawrence River. Since 1993, this index has shown a 99% decline in recruitment (Casselman 2003). Total annual eel passage, somewhat influenced by variable annual operating conditions, indicates only a very minor improvement in recruitment since 2003 (Figure 3). Assuming panmixia, Ontario's St. Lawrence River indices, at the extremities of the range, can be strong indicators of population-level change. These indices are among the most reliable since they are the longest and most consistently measured (Casselman et al. 1990). However, catch data across jurisdictions may be more or less sensitive to issues of hyperstability or hyperdepletion, depending on distance from the source of recruitment, and need to be interpreted carefully until appropriate population-level assessment programs are developed.

While diminishing abundance may be most pronounced at the extremities of the range in waters such as the USLR/LO, American eel appear to be in decline across North America (Petersen 1997; ASMFC 2000; Haro et al. 2000; Richkus and Whalen 2000; Casselman 2003). Key indicators of concern are (1) 99% decrease in eel recruitment to the USLR/LO (Casselman 2003); (2) indications that yellow eels are at historically low levels in the eastern United States (ASMFC 2006); (3) significant declines in silver eel harvests in Québec (Robitaille et al. 2003); and (4) declines in harvests in most of the commercial fisheries throughout North America, despite sustained high prices and strong demand in European and Asian markets. The general lack of long-term fishery-independent data series across the range has caused some to debate population status of American eel. In particular, the lack of reliable effort statistics is considered problematic as harvest trends can be driven by market conditions. While results may be misleading when effort is not taken into consideration, changes in commercial harvest can be interpreted much more precisely by taking price into consideration (Casselman and Marcogliese 2007).

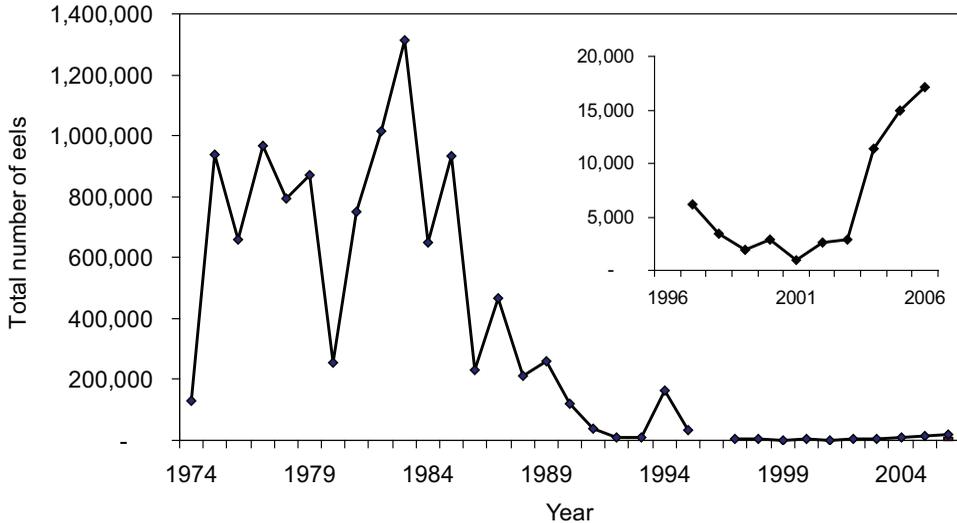


Figure 3.—Estimated number of eels annually ascending and exiting the Moses-Saunders eel ladder, Cornwall, Ontario, 1974 to 2005, and Moses-Saunders and New York Power Authority (Massena, New York) eel ladders combined, 2006 (inset 1997 to 2006). Numbers of eels represents total passage, not a standardized index of abundance because of variability in operating conditions. Operation of Moses-Saunders eel ladder varied greatly among years (33 to 154 d), and two ladders were used in 2006.

Habitat Loss and Mortality Due to Barriers

Construction of barriers has reduced eel access to a large portion of formerly important freshwater habitat. From Maine to Florida, at least 15,115 dams restrict or prevent fish passage, leaving up to 84% of Atlantic coast river and stream habitat inaccessible (Busch et al. 1998). While this estimate assumes a worst-case scenario of 100% blockage at the first dam, a succession of barriers on a watershed will no doubt accumulate their effect. The majority of dams on Atlantic coastal rivers in the United States have no provision for fish passage (Haro et al. 2000). There also are numerous examples of lost habitat due to dams within the Mississippi River basin and other watersheds of the Gulf of Mexico. The situation is similar in Canada. For example, the St. Lawrence River basin, which constitutes about 19% of American eel freshwater habitat, contains some 8,411 dams (Verreault et al. 2004). These dams are estimated to block access to 12,140 km of eel habitat in the St. Lawrence River watershed (Verreault et al. 2004). There are 5,260 dams in Quebec watersheds alone that drain

into the St. Lawrence River. In this watershed, as in much of North America, dam construction increased in the early 1900s and peaked between 1950 and 1970 (Figure 4).

Impacts of Hydroelectric Facilities and Other Barriers

Hydroelectric dams affect eels by forming barriers to upstream movement by young eels and subjecting silver eels to turbine mortality as they immigrate to the ocean (McCleave 2001; ICES 2003, 2006; Allen 2008). Young eels are able to use damp substrates to maneuver around obstructions (Haro et al. 2000), and locks, ditches, and marshes can provide limited passage. While some dams may be only partial obstructions, successive dams will have a cumulative impact on upstream passage of juvenile eels and will limit or completely restrict access to important rearing habitats. To illustrate, White and Knights (1997) found that dams on rivers had a greater effect on European eel than distance from the ocean, resulting in the upstream habitats being practically deserted.

As illustrated in early reports, dams have long affected American eel. Numerous late 19th and

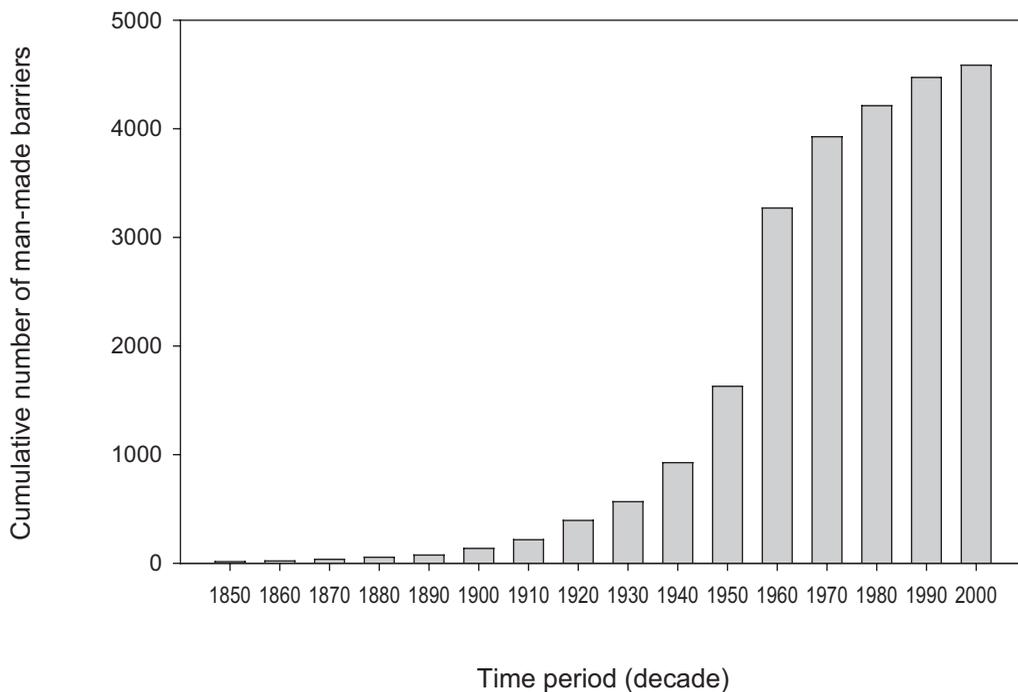


Figure 4.—Cumulative number of man-made barriers greater than 1 m in height in Quebec watersheds of the St. Lawrence River, plotted over time period (1850 to 2005). Data were obtained from the Centre d’expertise hydrique, Ministère du développement durable, de l’environnement et des parcs, Gouvernement du Québec.

early 20th century accounts reference the mortality of eels due to turbines and mill wheels in the eastern United States (The New York Times 1886, 1891, 1895, 1900, 1908) and in Michigan (Ballard 1948). Early 20th century accounts document mortality at mills within the Ottawa River watershed in Canada (Burnett 2007). Indeed, The New York Times (1906) reported that eels had become so abundant in the Connecticut River at a “local electric light plant” that they clogged the wheels and eventually stopped them. While these references imply the negative effects of eels on mill and power production, they also provide evidence of former eel abundance and indicate that this type of mortality problem has occurred for more than a century, likely increasing in significance as hydroelectric technology increased. As recently as the 1970s, eel mortalities due to turbines were so highly visible in the St. Lawrence River that Ontario Hydro annually hired contractors to pick up and dispose of metric tons of eel carcasses below the Ontario side of Moses-Saunders Dam (Verreault and Dumont 2003; J. M. Casselman, unpublished data).

Provisions for safe downstream passage of eels at hydroelectric facilities are rare, and turbine mortalities of downstream migrants can be high. Numerous successive facilities on a particular watershed will increase cumulative mortality. Donnil et al. (2001, in ICES 2003) estimated an average annual mortality of 92.7% for European eel in the River Rhine for a succession of 12 hydroelectric facilities. Cumulative turbine mortality at the two hydroelectric power facilities on the St. Lawrence River is calculated to be more than 40% (Desroches 1995; Normandeau Associates Inc. and Skalski 1998). Smaller turbines such as those on the Ottawa and Trent River systems likely induce higher eel mortality as it has been shown that eel survival increases with increasing turbine size (Lariniere and Dartiguelongue 1989).

Eel size may also influence mortality rate. Haro et al. (2000) estimated turbine-induced injuries as high as 50% for small eels and up to 100% for large eels. Increased vulnerability of large eels is particularly troubling as females are larger and pre-

dominant in the upper reaches of watersheds. In a simulation model of the cumulative effect of 13 power stations on the Kennebec River in the United States, McCleave (2001) predicted that only 40% of the female eels would reach the ocean, assuming a 20% mortality rate at each facility, and this estimate did not consider fishing mortality. American eel travel far to reach the upper St. Lawrence River, Lake Ontario and associated inland waters, where they grow and mature for 12 or more years (Casselman, unpublished data). Eels from these waters are virtually all female and traditionally have produced the largest and most fecund females within the species' range (Casselman 2003). While estimates and modeling are still preliminary (COSEWIC 2006), these females undoubtedly made a substantial contribution to the reproductive potential for the entire species (Casselman 2003; Verreault and Dumont 2003). Given impacts on females in freshwater systems, the cumulative lost fecundity from North American freshwater watersheds due to dams cannot be overlooked.

Case Histories of Significant Habitat Loss Due to Barriers

Extensive habitat loss due to barriers has occurred throughout the American eel range. Examples spanning much of the North American range include the Richelieu River in Québec, the Oswego River–Oneida River system in Lake Ontario, and the Susquehanna River in Maryland. In the Richelieu River and Oswego–Oneida systems, harvests in the early 20th century regularly approached 70 and 100 mt, respectively, but now due to the construction of dams, eels in both systems are exceedingly rare (Adams and Hankinson 1928; Henke 1993; Axelsen 1997; Lary et al. 1998; Verdon et al. 2003; Verreault et al. 2004). In the Susquehanna system, eel harvests averaged some 393.4 mt annually prior to the construction of the Conowingo and three other main-stem dams in the 1920s. The commercial harvest since then has been zero, and it is estimated that there are 11 million fewer eels in the Susquehanna today than in the 1920s (MdDNR 1999).

To these examples, we add new evidence of dam-related habitat loss in inland Ontario. Archaeological, historical, and anecdotal information from the Ottawa and Trent rivers reveal surprising abundance of eels, a fact long since forgotten in the

absence of readily accessible information. However, more recent commercial harvest and fishery-independent information illustrates the extent of habitat loss and reductions in eel distribution in these watersheds. Thus, these examples represent a pattern in habitat loss and shifting baselines that appears widespread across the North American range as eel diminished over the past century

The Ottawa River watershed is large, encompassing a drainage area of 146,000 km², representing about 12% of the St. Lawrence drainage area, including thousands of lakes in Ontario and Québec. An estimated 3,700 km² of suitable habitat was present within this system before extensive dam construction throughout the watershed (Verreault et al. 2004). Eels historically were abundant within this system (Small 1883) and penetrated the river as far inland as Lake Timiskaming (Purvis 1887), 580 km from its confluence with the St. Lawrence River. Archaeological evidence shows the presence and heavy use of American eel in the Ottawa River watershed by indigenous peoples, dating back some 4,000 years (Clermont and Chapdelaine 1998; Clermont 1999; Clermont et al. 2003). In the early 1900s, eels remained sufficiently abundant in the Ottawa River to support important commercial fisheries in Ontario and Quebec waters. Dymond (1939) notes that Quebec commercial eel harvests from the Ottawa River always exceeded those from Ontario; Quebec harvests ranged from 3.4 to 15.0 mt annually between 1930 and 1937.

This watershed has been heavily affected by fragmentation, first by the development of sawmills to support a burgeoning timber industry and later by numerous large hydroelectric installations (OMNR/Québec MNRF 1999; Haxton and Chubbuck 2002). The first hydroelectric dam was installed on the main branch of the Ottawa River at Chaudiere Falls (Ottawa/Hull) in the 1880s, and the ninth and final large dam on the main branch was constructed in 1964 at Carillon. Many more facilities were installed on tributaries within the watershed (Figure 5), making the system one of the most highly regulated watersheds in Canada (Telmer 1996).

American eel subsequently declined throughout the Ottawa River watershed. Historically abundant throughout the Mississippi River, a tributary of the Ottawa River, many were sampled during netting projects as late as the 1960s, but now are rarely

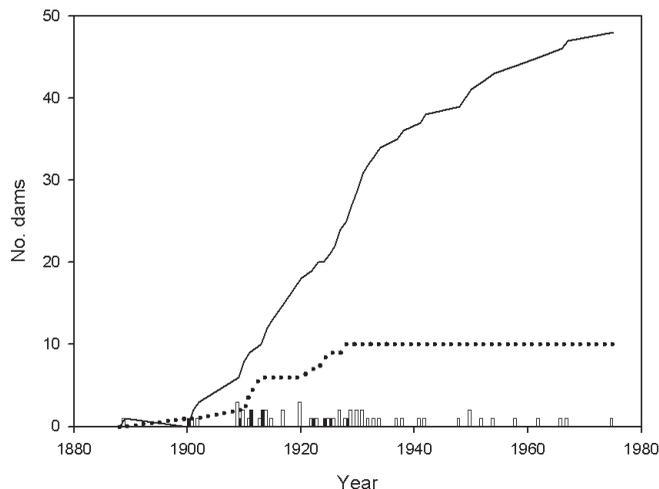


Figure 5.—Number of dams (open bar—Ottawa River; solid bar—Trent River) and cumulative number of dams (solid line—Ottawa River; dotted line—Trent River) constructed on the Ottawa River watershed or Trent River, 1880s to 1970s.

captured (Figure 6; Ontario Ministry of Natural Resources, unpublished data). The last American eel was reported from Algonquin Park in 1936 (Mandrak and Crossman 2003). Locks in the lower Ottawa River enable some immigration into the lower watershed. Eels are still found within the Ottawa River as far upstream as the Bonnechere River/Lac

des Chats (260 km from the St. Lawrence River), but only as a remnant of their former abundance (Figure 7; T. Haxton, Ontario Ministry of Natural Resources, unpublished data). Four Ontario commercial fishing licenses remain in the lower Ottawa River, but prior to the Ontario eel closure in 2004, only a few hundred kilograms of eels were harvested

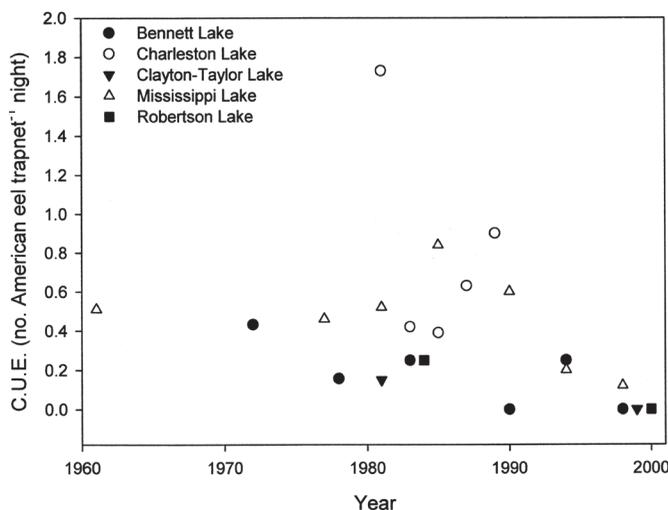


Figure 6.—Catch per unit effort (CPUE) of number of eels caught per night of trap netting in five lakes tributary to the St. Lawrence River or Ottawa River, Lanark County, 1961 to 2000. Fish-passage facilities do not exist at any dam. Data exist only for the years indicated.

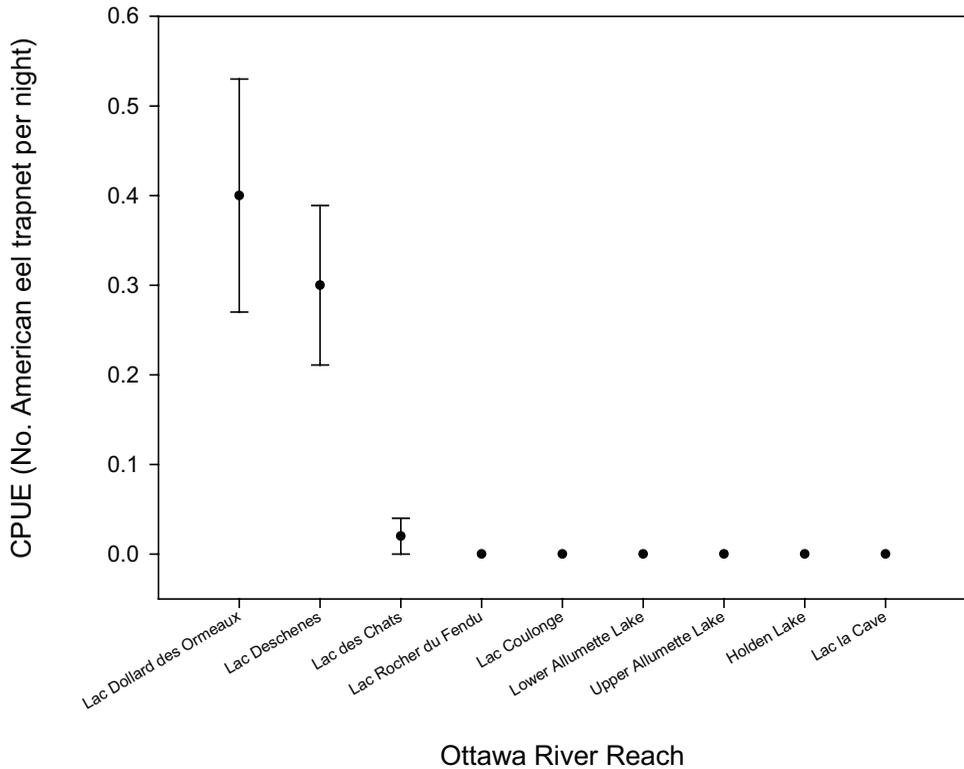


Figure 7.—Catch per unit effort (CPUE) of number of eels caught per night of trap netting in reaches of the Ottawa River, progressively farther upstream. Lac Dollard has the first upstream barrier, and the first reach is defined as below Lac Dollard des Ormeaux. Each additional barrier upstream defines the next reach as the area between dams. Vertical lines indicate 95% confidence limits.

annually (Ontario Ministry of Natural Resources, unpublished data).

Eels also were historically abundant in the Trent River watershed of Lake Ontario. The basin encompasses some 218 shallow and productive lakes in the Haliburton Highlands and Kawartha Lakes regions, which afford excellent eel habitat. As for the Ottawa River, there are historical and archaeological records of eel presence and use in the Trent River watershed. There is evidence that indigenous peoples had fish weirs in the system (Fraser 1912); stakes from an apparent fishing weir in Lovesick Lake was carbon-dated to more than 6,000 years old (Stevens 2004). Eel vertebrae were present in numerous test units at the significant precontact Late Woodland Gibson Site (BcGo-14) on the south shore of Chemong Lake near Peterborough, Ontario (Archaeological Services Inc. 2008). Copway (1847) noted that “Rice Lake contains quantities of the finest fish...

bass, eels, etc. are also found in this lake.” The Reverend Peter Jacobs (1857) described Rice Lake as one that abounds with “muskinooj, bahs, eels.” In 1817, fish weirs in the lower Trent River captured eels, whitefish, and other species (Fraser 1912). An advertisement in the Coburg Star (1838), marketing a mill property on the Otonabee River near Peterborough, Ontario provides further evidence that eels were abundant and valuable in the upper Trent River watershed. Among other selling points, the ad featured close to 50 £ sterling worth of eels that “were taken last season in the boxes fixed in the saw-mill.”

In the late 1800s, commercial eel landings from counties surrounding the Trent River watershed ranged between 2.1 and 11.4 mt, annually (Canada 1885, 1886, 1887, 1888, 1889b, 1900). This system was first fragmented by mill dams, followed by the construction of the Trent-Severn

Waterway in the late 1800s. The waterway initially consisted of a series of dams and locks to aid navigation and was further altered between 1900 and 1928 with the addition of 14 hydroelectric facilities (Figure 5). None of the generating stations provide fishways, although a series of locks at each dam provides some upstream access. American eel have been virtually extirpated above the first barrier, and the last few were recorded by assessment gear in the Kawartha Lakes in the mid-1980s (Ontario Ministry of Natural Resources, unpublished data).

Beginning in the early 20th century, eel abundance and distribution have declined substantially in response to decades of barrier construction across the North American range. Losses have been gradual over this period, leading to fading memories of the former presence and importance of this species. As noted earlier, perspectives on the importance of eels clearly shifted over the same period, leading to spotty record-keeping and low priority in fisheries management. Today, it often comes as a surprise that eels were even present, much less important, in many watersheds where they are now rare or absent.

While recent sharp declines in abundance have been detected in the late 20th century, it is clear that lost eel production began at a much earlier time. Major barrier construction began in the early 1900s and appears to have peaked in the 1950s-1960s. Given the long life span of eels in many freshwater systems and the unique panmictic life cycle, the cumulative effects of barrier construction would take a considerable amount of time to become apparent. The effects would manifest themselves through lost production from formerly accessible and productive habitat and would accumulate over many years at the population level. Thus, the accrued losses in spawner production from freshwater systems and effects on subsequent recruitment are particularly concerning.

Discussion

While the European Union has accepted that there are substantial declines in the European eel (EU 2007), there remains debate in North America regarding the status of American eel, despite the warnings by Casselman (2003) and Dekker et al. (2003). The evidence presented indicates that eels, particularly in freshwater habitats, have been severely marginalized due to anthropogenic impacts over the past century.

Population-Level Declines

Our extensive review of historical, traditional, and commercial harvest statistics indicates that American eels were formerly much more abundant in North America at the time of European contact. In more recent decades, commercial harvest statistics across the North American range have shown major declines despite sustained strong markets and high price. Long-term recruitment indices are rare, but as juvenile eel dispersal appears to be influenced by density, we are concerned that the recruitment indices in the USLR/LO (near the extremity of the range) may indicate population-level recruitment declines to continental waters.

Many fishery-independent indices for American eel across North America were not originally intended to target eels, are relatively recent, and often may not span an adequate time period, particularly in the case of recruitment indices. For instance, if only the most recent 15 years of the USLR/LO recruitment index were to be examined, one would erroneously conclude stable conditions, whereas eel recruitment had actually declined by 99% since the late 1980s (Figure 3). However, fishery-independent indices for the USLR/LO extend back into the early 1980s, and these indices point to a substantial decline in yellow eel abundance that parallels the steep decline in recruitment to these waters. This information, combined with the observation that yellow eels are at or near historic lows across the eastern seaboard of the United States (ASMFC 2006), matches the observed sharp declines in commercial harvests across North America (Figures 2A-C). While declining expectations and shifting baselines have clouded today's perceptions of American eel status, there is little doubt that American eel abundance has declined significantly over the past century, becoming particularly concerning over the past 20-30 years in many formerly significant components of its range.

Distribution Change

It is clear that eels formerly were distributed widely across all accessible freshwater habitats in eastern North America, ranging throughout watersheds and coastal habitats associated with the USLR/LO (including large systems such as the Ottawa River), eastern North America, and gulf states through to the upper Mississippi River (COSEWIC 2006; NatureServe 2007). We have described substantial,

formerly highly productive areas where eels have been virtually extirpated and other areas where abundance obviously has declined significantly. These areas are all associated with the construction of numerous dams. This evidence suggests that cumulatively, dams have been a major cause in eel declines by reducing eel production and subsequent recruitment at the population level.

The extent of habitat loss has been substantial, with few large watersheds free of barriers. Adding to these concerns are observations that all of these waters formerly supported abundant production of predominantly large, highly fecund females. The examples of lost habitat documented herein appear symptomatic of a widespread problem across the North American range where significant lost eel production has occurred throughout the freshwater range, wherever major barriers have been constructed. Significant mortalities of predominantly female eels at hydroelectric facilities pose additional concern, especially when the mortalities are cumulative across a number of utilities on a single watershed (e.g. Ottawa and Trent River watersheds in Ontario).

Importance of Life Cycle Diversity and Panmixia to Management and Conservation

The science to date supports that American eel are panmictic (Avisé et al. 1986; Wirth and Bernatchez 2003); therefore, it is particularly important to view the dynamics of American eel at the population level. For instance, if eels are panmictic, the consequences of lost female production in freshwater systems due to lost habitat combined with the costs of mortalities due to turbines and fishing would be additive and substantial on one common spawning stock. The protection of spawners and spawning habitats is particularly crucial in the management of long-lived species (Winemiller and Rose 1992) like eels. It is evident that spawner biomass of eels has declined over the past century. Under a model of panmixia and density-influenced dispersal of recruits, there would be direct negative feedback in terms of lower spawner biomass and reduced continental recruitment in the future (Casselman 2003). If geographic dispersal of recruits is influenced strongly by density, it would not be surprising to see stock indicators nearer to the source of recruitment remain apparently stable for a period of time while they collapsed in more distant waters.

Environmental variations also may induce recruitment vacillations in the American eel population (e.g., changes in oceanic productivity and currents, Beak 2001; Friedland et al. 2007; Bonhommeau et al. 2008). Cumulative anthropogenic effects, including overfishing, turbine mortalities, and lost habitat, may have destabilized the American eel population and increased its sensitivity to environmental conditions (Bonhommeau et al. 2008). Recruitment fluctuations due to environmental change highlight the need for improved escapement of spawners to boost reproductive output, hedging against environmentally induced periods of poor recruitment. Many diadromous fish populations use multiple modes of migration and habitats (McDowall 1996), and divergent migration behaviors or habitat use can reduce the overall variance of population responses to environmental change, thereby increasing stability and resilience. Termed “contingents” for eels and other species (Secor 1999; Jessop et al. 2002) in the concept of stock, multiple life cycles can induce a dampening effect on overall variance of population responses to environmental change, thus increasing stability and resilience.

Contingent structure has been shown for Japanese eel *Anguilla japonica*, European eel, and American eel (Tsukamoto et al. 1998; Tzeng et al. 2000; Tsukamoto and Arai 2001; Jessop et al. 2002; Morrison et al. 2003). In the case of American eel, at least two contingents can be visualized: one in which yellow eels predominately grow in freshwater; the other growing in marine habitats. These divergent life cycle pathways confer resiliency against spatial variation in mortality risk, and in the extreme case, if one contingent should fail, the other contingent would persist as an effective means of bet-hedging (Secor and Kerr 2009, this volume). Further, as eels mature at different rates across a wide variety of latitudes, and multiple cohorts from a widely diverse set of habitats apparently spawn together in any given year, overlapping generations can also contribute to population persistence. Here, strong recruitments are figuratively stored in the adult population (Secor 2007). At high latitudes in freshwater, eels primarily are long-lived, highly fecund females (Lary et al. 1998). Thus, protection and restoration of freshwater contingents will serve to improve American eel resiliency to further, seemingly inevitable anthropogenic disturbances and ensure sufficient population-level fecundity.

The evidence presented suggests that during the

past century the contribution of the freshwater contingent of American eels has been substantially marginalized by anthropogenic effects. As human population and development increase, impacts on both freshwater and marine systems will continue (Lackey et al. 2006a, 2006b). Our review suggests that it is imperative to restore and maintain the freshwater contingent to sustain resilience against future perturbations. The strictly marine segment of the population requires further study. While less understood, it is clear that the estuarine habitats can be particularly productive for eels and that the marine contingent may make important contributions to the overall population. Some of these habitats may not have been altered as much as freshwater ecosystems, and they are no less important to protect from overexploitation and further degradation. However, given that American eels extensively use all accessible freshwater habitats, it is ill-advised to discount the importance of freshwater eels on the premise that the marine contingent will sufficiently protect the species. This is especially important given the dominance of females in the freshwater contingent. Preserving only the most productive habitats may be a flawed management strategy (Kraus and Secor 2005). Rather, priority setting should be based on studies of habitat use that match the generation time (Secor 2007).

Constituent patterns of life cycle diversity within populations should be regarded as a portfolio that hedges against future environmental uncertainty (Secor and Kerr 2009). Conservation and recovery planning exercises need to recognize the diverse life cycle of American eel, the cumulative nature of impacts, and the importance of protecting and restoring their portfolio of habitat types. Contingent structure, proximity to the source of recruitment, and higher eel productivity in estuarine habitats may help explain differing views of American eel status. Edeline (2007) proposes that the decline in European eels could be less steep in saltwater than in freshwater habitats, suggesting that eel diadromy may be a conditional strategy and that anthropogenic changes are acting selectively on freshwater habitats.

Necessity for Coordinated Conservation and Management Actions

In the past, little attention was given to silver eel escapement in American eel management, apparently as a consequence of management perspectives

described earlier, regional approaches, and absence of population-level assessment. Difficulties with fish stocks often occur when it is assumed that the number of spawners has little to do with subsequent recruitment (Clover 2006). Inadequate attention to spawning stocks is a common problem in fisheries science and management (Walters and Maguire 1996). In this context, the collapse of juvenile recruitment to the USLR/LO just a few years after the record-high North American harvests, and a decade or two after the peak in dam construction, is disconcerting.

Depensation was implied tentatively by Dekker (2008) for the European eel and may be an issue for the American eel. If the index of recruitment to the USLR/LO reflects existing or forthcoming continental declines, depensatory pressures may add significant hurdles to recovery efforts if actions are not undertaken soon. Thus, future management initiatives should carefully consider the cumulative consequences of fishing and turbine mortalities on subsequent spawner biomass and recruitment. Strongly coordinated strategies to significantly improve silver eel escapement appear essential.

The impacts of significant widespread loss and fragmentation of freshwater habitat, primarily due to dam construction over the past 150 years, again are cumulative at the population level. While some American eel appear to complete their entire life cycle in brackish estuarine habitats (Lamson et al. 2006), it is clear that eels have made extensive use of freshwater habitat across their range, producing predominantly large females. Therefore, both habitats play critical roles, and both contingents merit protection.

The recently renewed interest in hydroelectric power, combined with growing eel markets, will add pressure on the population unless mitigation measures are implemented. It is clear to us that strong, coordinated conservation actions are required, with the ultimate objective of vastly improved silver eel escapement and recruitment. Further loss of eel habitat should be unacceptable, and existing levels of anthropogenic mortalities do not appear to be sustainable. Rather, improved access to formerly productive habitats is necessary, as are coordinated and strategic reductions in mortality due to fishing and turbines. Finally, given apparently reduced continental recruitment, harvests of glass eels and elvers need to be closely managed and coordinated.

Recovery Planning

The evidence presented herein suggests cause for concern at the population level and the need for immediate development and implementation of recovery plans. The absence of long-term stock assessment data should not be a deterrent to taking appropriate actions; rather, this situation requires adopting a precautionary approach until better information is available. Clearly, sharp increases in total anthropogenic mortality have occurred over the past century, accumulating in their effects at the population level. Largely as a result of the panmictic nature of eels, regional approaches to eel management have not been successful. For example, thousands of dams have been constructed over the past century with little consideration of their cumulative, population-level impacts on eels and other diadromous fishes. These structures were evaluated on a case by case basis over several decades; environmental impacts would only have been reviewed in the site-specific context. Similarly, eel fisheries have been managed independently across numerous jurisdictions, with little consideration of the population-level context.

More recently, some jurisdictions recognizing eel declines have undertaken some actions to protect American eel, but it is difficult for one or only a few jurisdictions to implement effective conservation measures given the panmictic nature of eels (MacGregor et al. 2008). As early as 1980, concerns over mortalities due to fishing and turbines prompted convening the North American Eel Symposium (Loftus 1982). While some expressed concern over increased mortalities (Kolenosky and Hendry 1982), others thought differently, assuming that (1) there was no reason why every silver eel should not be harvested since fisheries were localized and numerous areas fished either lightly or not at all, (2) escapement of adults from a few stocks could sustain the species, (3) silver eels represented a loss of organic material from freshwater since they spawned and died in the sea, and (4) silver eels would be lost from the fishery anyway (Eales 1968). With such conflicting opinions, there was little interest in developing a coordinated management plan for eels in North America at that time (Loftus 1982).

However, by 2005, the Committee on the Status of Endangered Wildlife in Canada reviewed the Canadian status of the American eel and recommended a designation of "special concern" (COSEWIC

2006). In Ontario, the Committee on the Status of Species at Risk in Ontario recommended a designation of "endangered" under Ontario's Endangered Species Act, and the species was officially listed on July 1, 2008 (OMNR 2007). In contrast, protection of American eel under species at risk legislation in the United States has not occurred to date. A recent petition to list American eel under the federal Endangered Species Act (Watts and Watts 2004) was unsuccessful (U.S. Office of the Federal Register 2007). American eel is not formally listed at this time as endangered or threatened in the U.S. under the federal Endangered Species Act, nor is it listed under the National Marine Fisheries Service's Species of Concern Program, a proactive conservation program for species that may become threatened or endangered.

Canada has announced the development of a national management plan to reduce anthropogenic mortality of American eel by 50% (DFO 2004). Further development of the plan and implementation of actions are underway (MacGregor et al. 2008). In the United States, the Atlantic States Marine Fisheries Commission has developed a management plan for American eel (ASMFC 2000), and fish passage plans have been developed to improve access for eels and other diadromous species to the important Susquehanna River watershed (PFBC 2007; MdDNR 2008; Native Fish Conservancy 2008). Binational efforts have begun to set the scene for recovery of the USLR/LO segment of the population under the auspices of the Great Lakes Fishery Commission.

A model developed by Beak (2001) was sensitive to the cumulative effects of anthropogenic mortality (fishing and turbines) on resident eels and to the effects of habitat exclusion by dams. The modeling exercise further suggests that the provision of high efficiency upstream passage facilities and mitigation of downstream passage at hydroelectric facilities could confer substantial benefits to egg production from Lake Ontario and St. Lawrence River eels (Beak 2001). In Canada, it now is considered critical that restoration efforts focus on substantially improved escapement of silver eels and that recovery plans be implemented using strategic watershed approaches involving improved access, reduced mortality, and increased escapement. The recently approved European Union regulation for European eel also has determined these approaches to be essential (EU 2007).

A range-wide approach for American eel recovery planning is warranted (Dannewitz et al. 2005;

MacGregor et al. 2008). While progress in both Canada and the United States has been made in moving away from uncoordinated regional approaches (ASMFC 2000; DFO 2007), the most appropriate model would be binational in scope (MacGregor et al. 2008). Formal discussions between Canada and the United States are underway to develop an effective memorandum of understanding among agencies that will establish coordinated binational management and science across the existing North American eel range. The adoption of a broad ecosystem approach covering a range of habitat and mortality issues will be an underlying theme.

Summary

Any person stand[ing] on the banks of the Delaware...at this season of the year will see at what first sight appears to be a huge serpent moving up the stream near the shore. If the spectator wishes to see the end of this moving mass, he must remain...for three or four days...he will be surprised upon investigating... [that this] endless line of life...is made up of the diminutive eels. (The New York Times 1880b)

The formerly massive recruitment events reported in earlier times (The New York Times 1880b; Hartford Courant 1902) now rarely occur, and eel declines across North America are evident. We have shown that watershed by watershed, American eel gradually have declined or disappeared in numerous formerly productive waters, at times almost invisibly. Anthropogenic mortality and the harmful alteration and disruption of habitat have had cumulative, insidious, and substantial effects on the American eel population over the past century. In particular, the 1950–1970 peaks in dam construction and turbine mortalities, together with the unprecedented North American harvests in the 1970s, have led to a perilous synergy of effects at the population level. Conservation and restoration efforts are long past due.

Overseas markets for American eel are expected to remain high in response to significant declines in European and Japanese eels and in response to new conservation measures implemented by the European Union (EU 2007). In addition, anthropogenic stresses will mount as human population growth continues. Under these circumstances, pressures to

develop more renewable energy sources such as hydroelectric power can be expected to increase, as will pressures to maximize harvests of American eel. Difficulties in implementation of recovery measures will be exacerbated significantly if mitigation and conservation policies that address cumulative impacts are not executed soon.

While recovery efforts targeting full restoration to former abundance levels are likely unrealistic, timely efforts are required to halt the decline and prevent potential compensatory effects. The protection and restoration of freshwater and marine contingents are equally important to ensure population resilience and guard against future anthropogenic stressors. Conservation and recovery efforts are not only necessary to ensure long-term sustainability of the resource, but are also necessary to ensure preservation of the long-standing economic, ecological, cultural, and natural heritage values of this species. Measured, strategic steps across the North American range are required in a coordinated fashion.

Traditional ecological knowledge and anecdotal, historical, and archaeological information have been useful in establishing a baseline understanding of former eel abundance and distribution and will be very useful in recovery planning. Whatever the shape of the ultimate recovery prescription, it is clear that the recognition of rights and interests of indigenous peoples and stakeholders need to be incorporated appropriately. Finally, the circumstances of American eel should be viewed as symptomatic of the challenges faced by many diadromous fish species in North America; cumulative effects at the species level should not be overlooked.

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