

**EARLY CHANGES
IN THE FISH COMMUNITY
OF LAKE ONTARIO**



Great Lakes Fishery Commission

TECHNICAL REPORT 60

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April 1995

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OF LAKE ONTARIO**

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Great Lakes Fishery Commission
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FOREWORD

Stanford (Stan) Smith wrote this paper shortly after he retired from the U. S. Fish and Wildlife Service in 1972. It was reviewed shortly thereafter by Vernon Applegate, Paul Eschmeyer, and Dwight Webster. Never formally submitted to a journal, the manuscript then languished for two decades. I felt that Stan's treatment of the early history of the Lake Ontario fish community would be of keen interest to our readers. No effort has been made to update references and the paper should be interpreted in relation to when it was written. Of major interest and not dated, however, are Stan's treatment of the early accounts of the alewife and sea lamprey in Lake Ontario. Few researchers are prepared to invest the time that he did in scouring old sources of information that bear on important events in the ecology of the Great Lakes. Belated publication of this paper is in recognition of these efforts and of his involvement with and commitment to the Commission's philosophy and program.

R. L. Eshenroder
14 February 1995

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ABSTRACT. Lake Ontario may have had the highest fishery yields of any of the other deepwater Great Lakes, but these catches occurred before the mid-1800s - before catches were recorded. The Atlantic salmon (*Salmo salar*) was the most-valuable species in the early fishery and was severely depleted before a quantitative account of the fishery could be made. Drainage modifications also contributed to the extinction of salmon in Lake Ontario; by 1845, a total of 7,406 water-powered sawmills were being operated in the state of New York. Forest removal further degraded spawning and nursery streams and affected recruitment of obligate and facultative stream spawners. The alewife (*Alosa pseudoharengus*) probably invaded Lake Ontario from the Erie Canal. By the late 1800s, the alewife was associated with declines of planktivores and piscivores, a pattern that occurred in the upper lakes in the mid-1900s. A close examination of early accounts of the sea lamprey (*Petromyzon marinus*) in the Lake Ontario watershed shows that the first reliable sighting was in 1835. Misidentification of the sea lamprey resulted in reports that it was endemic to the lake. Sea lampreys probably gained access to the lake from the Erie Canal, but because of degraded stream conditions, they did not become abundant in Lake Ontario until after the early 1900s when lake trout (*Salvelinus namaycush*) stocks collapsed.

INTRODUCTION

The progressive changes in the fish populations of the Laurentian Great Lakes (Fig. 1) have provided a sensitive measure of the consequences of the influence of man's activities on a stable and productive fish community. Less than two centuries ago, there was an abundance of fish throughout the Great Lakes, their bays, marshes, and tributaries. At the present time, almost all of the previously abundant species are

either greatly reduced or extinct in part or all of their former range. New species that were introduced or invaded the lakes, or native species that were not formerly abundant, have increased as other species have declined. However, they have not replaced the previously abundant species in kind, usefulness, or quantity. The result is reduced fish biomass and increased instability of the fish stocks which underwent increasingly rapid changes.



Fig. 1. The Laurentian Great Lakes showing canals that allow passage of fish into and between the lakes.

The primary cultural factors that influenced fish stocks have been:

- Intensive and selective exploitation that has been directed toward the most-preferred species.
- Filling and dredging within the drainage basin modified shore areas and swamps.
- Major changes in the characteristics of the drainage basin strongly influenced the environmental characteristics of tributaries.
- The creation of entrance routes from the ocean and between lakes that facilitated the invasion and dispersal of marine species.
- Degradation of the environment made portions of lakes, and as a result, entire lakes unsuitable for the more-valuable native species.

Usually two or more of these factors influenced the same fish stock at one time, making it difficult to evaluate the responses of fish to each factor. Because different factors or combinations of factors were prevalent in different lakes or sections of a lake at different times, it is possible to draw inferences about the sensitivity of various species to each factor (Smith 1972a).

The sequence of reaction among families of fish and species within families has been the same when various factors became prevalent at various times and locations. This replication tends to give additional credence to suspected cause-and-effect relations. The Laurentian Great Lakes provide a unique situation in this respect because the lower (eastern) lakes were influenced earliest by the effects of man and of invading marine species. The upper (western) lakes were affected later. Therefore, similar sequences of events have moved through the lakes from east to west during the past 150 years. These events, which were more recent in the upper Great Lakes, permit greater insight into the less completely described or documented events that occurred in the lower lakes many decades earlier.

The chain of events that caused disruptive changes in fish communities of the Great Lakes started with modifications of the Lake Ontario drainage basin. The modifications contributed to the decline and extinction of the Atlantic salmon (*Salmo salar*). The modifications also allowed the subsequent invasion and establishment of the alewife (*Alosa pseudoharengus*) and the sea lamprey (*Petromyzon marinus*). Intensive selective exploitation and water-quality degradation had major independent

influences on fish stocks. They also had substantial catalytic effects that accentuated or accelerated other influences and their consequent biotic disruptions. Of these events, the most-traumatic consequences were related to the invasion, establishment, and dispersal of the sea lamprey throughout the Great Lakes. The sea lamprey became a new dominant climax predator in all lakes except Erie and initiated a major disruption of fish communities in the various lakes. This review of early conditions and changes in the Lake Ontario drainage reflects, in general, the events that occurred in the other lakes.

Detailed discussions of the fisheries and events in each of the Great Lakes are covered in the proceedings of a symposium on Salmonid Communities in Oligotrophic Lakes held in Canada in 1971 (Loftus and Regier 1972) and ensuing papers (Berst and Spangler 1973; Christie 1973; Hartman 1973; Lawrie and Rahrer 1973; Wells and McLain 1973).

EARLY CONDITIONS

Before extensive exploitation by immigrants (primarily from western Europe) the natural resources of the Laurentian Great Lakes were described in glowing terms. Most of the drainage was covered by dense forests. Many swamps were dispersed throughout the drainage and along the lake shores. Rich meadows were scattered throughout the forest-particularly in the flatter areas of the upper Great Lakes (Thwaites 1896; Hedrick 1933; Trautman 1957). The water of Lake Ontario was described in 1749 as, "very transparent; at 16 and 18 feet, the bottom can be seen as if one saw it through polished glass." It also had the "property . . . of retaining great coolness" (Thwaites 1896). This description is typical of early comments about the physical characteristics of the waters of each of the Great Lakes. The tributaries of the Great Lakes were generally described as "clear lively streams" that flowed "brimming full" (Hedrick 1933; Trautman 1957). Snows that remained in the dense forests until late spring (Thwaites 1896) and a "profusion of springs," in addition to the many swamps, maintained high stream flows throughout the year (Trautman 1957).

A great abundance of fish occurred throughout the Great Lakes. Early descriptions indicate, with few exceptions, that species in the Great Lakes migrated into streams to spawn (Thwaites 1896; Trautman 1957). Coregonids and salmonids constituted the largest components of the fish population of each of the lakes, which reflected their oligotrophic character. The Atlantic salmon was the most-important piscivore in Lake Ontario where it occurred in great abundance in the lake and throughout its tributaries (Jones 1851; Edmunds 1874; Smith 1892; Follett 1932). The Atlantic salmon did not

occur in the other Great Lakes because Niagara Falls, between Lakes Ontario and Erie, prevented movement of fish to the upper lakes. The lake trout (*Salvelinus namaycush*) was an abundant piscivore in all the deepwater Great Lakes (Ontario, Huron, Michigan, and Superior) and abundant only in the deeper eastern section of Lake Erie (Smith 1972a). The burbot (*Lota Lota*) was a non-salmonid piscivore that was very abundant in all of the lakes.

The planktivorous coregonids constituted the greatest fish biomass in all of the Great Lakes. The large-bodied lake whitefish (*Coregonus clupeaformis*) and the smaller lake herring (*C. artedi*) were most abundant in the bays and shore areas of the deepwater Great Lakes and were particularly abundant throughout Lake Erie. Indeed, early descriptions and catch records indicate that the lake herring must have been the most-abundant individual species in each of the Great Lakes. Seven species of deepwater ciscoes (*Coregonus* spp.) constituted the greatest biomass in the deep regions of the four deepwater Great Lakes and were a major food of the lake trout and burbot. [The taxonomic status of one species of deepwater cisco, *C. alpenae*, is in doubt. *Ed.*].

The yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), walleye (*S. vitreum vitreum*), and blue pike (*S. vitreum glaucum*) were particularly abundant in Lake Erie. Except for the blue pike, all of them were abundant in the bays and shore regions of the deep lakes. The blue pike is believed to have reproduced only in Lake Erie (Christie 1973).

The more-abundant and widely distributed forage species of the Great Lakes were:

- deepwater sculpin (*Myoxocephalus thompsoni*) and slimy sculpin (*Cottus cognatus*) in the deeper areas, and
- the emerald shiner (*Notropis atherinoides*) and spottail shiner (*N. hudsonius*) in the shallower areas.

Collectively, these 19 species constituted the greatest number and biomass of fish in the Great Lakes. They represented the main components of what appeared to be a highly productive and stable fish community. There were, however, many other species that were not as widely distributed or abundant but were important components of the fish community in various lakes or sections of the lakes.

CULTURAL INFLUENCES IN LAKE ONTARIO

The Lake Ontario drainage was the closest to the eastern seacoast where immigrants landed in North America. In addition, the drainage was the earliest region in the Great Lakes to be influenced by human colonization. Although records are scattered and incomplete, the activities of man clearly exerted a major influence on the fishery resources of Lake Ontario prior to 1900. Substantial declines of many species occurred in the mid- 1800s (Goode 1884; Christie 1973). A survey of the Great Lakes fisheries during 1871 and 1872 (Milner 1874) reported:

From the information received from Lake Ontario, it is evident that the fisheries are more reduced than in either of the other lakes.

A report on the status of the Lake Ontario fisheries in 1897 (Cobb 1898) concluded:

Part of this decrease in the fisheries can be explained by the stringent laws governing the commercial fisherman but the main cause is the scarcity of fish.

Indeed, in the period after the 1860s for which there are fish-production data, Lake Ontario has generally been considered to have low fish productivity (Smith and Snell 1891; Christie 1973).

Descriptions of fish production during the early 1800s and data on the Lake Ontario fishery in the late 1800s (when compared with the other lakes) support the assumption that fish productivity during the period before major influences by man must have been as great or greater than in the other deepwater Great Lakes. According to Smith (1972b), the commercial production of 1.65 kg/ha from Lake Ontario recorded from 1879 to 1889, after substantial declines were described, was:

- 35% higher than the maximum production of 1.22 kg/ha in Lake Superior between 1940 and 1949, and
- 15% lower than the maximum production of 1.89 kg/ha in Lake Huron between 1900 and 1909.

Therefore, after a period of major decline (Milner 1874), the fish production from Lake Ontario on an areal basis was substantially more than one, and somewhat less than another of the two less productive of the Great Lakes during their period of maximum

yield. In recent years (1960-69), Lake Ontario-with a yield of 0.53 kg/ha---clearly had the lowest fishery production compared to the yields from the other lakes:

- Lake Huron-0.62 kg/ha,
- Lake Superior-0.69 kg/ha, and
- Lake Michigan-2.68 kg/ha.

If events in Lake Ontario prior to 1900 (before the period of production records) had the same influence on fish stocks that the same events had in Lake Huron (where they occurred in a later period when records of fish production were available) then Lake Ontario might have produced as much as 3.92-4.50 kg/ha during its period of high productivity (Smith 1972b). Lake Ontario would have been the most productive of the four deepwater Great Lakes. Many early descriptions of the fish populations and fisheries seem to verify that fish were once much more abundant throughout Lake Ontario and its tributaries (Jones 1851; Anonymous 1874; Thwaites 1896; Koelz 1926) than they were after production records first became available in the 1860s (Baldwin and Saalfeld 1962). Early production was particularly high on the south (United States) shore of Lake Ontario. Human colonization was more extensive there and organized commercial fishing increased earlier and was more intensive than on the north (Canada) shore (Smith and Snell 1891).

Exploitation

The seine fisheries that developed along the shores of Lake Ontario by the early 1800s were intensive and wasteful. The quantity of whitefish and other species taken in seines was described as “immense.” Whitefish were used as fertilizer (Adams 1912), and small whitefish, *lake* herring, and lake sturgeon (*Acipenser fulvescens*) were “destroyed as nuisances” (Koelz 1926). When fish became less abundant near shore, gillnets and trapnets were introduced to extend fishing into the open lake (Koelz 1926). Large catches continued until the sharp declines described in the mid- 1800s (Goode 1884).

Although whitefish and lake herring could be taken in large quantities and were fished abusively, the Atlantic salmon was undoubtedly fished most intensively because it was easily taken during spawning migrations. The Atlantic salmon was used less wastefully than other species because of its high value and excellent quality as a food source. Atlantic salmon were abundant in the lake throughout the year and adults were

present in the tributaries during much of the year (Jones 185 1; Anonymous 1874; Smith 1892). Salmon was a primary source of protein for the early settlers and military outposts. Sometimes the value of salmon runs was a basis for determining the value of land (Jones 185 1; MacKay 1963). Early Atlantic salmon fishing was undoubtedly most intense in tributaries. However, large catches were taken:

- from the lake after the introduction of pound nets around 1836 (Anonymous 1874; Smith 1892), and
- in deep water by greater use of gillnets after fish became rare in shore waters around 1860 (Koelz 1926).

Lake trout were not mentioned as prominently in early descriptions of the Lake Ontario fisheries as in the upper Great Lakes. This indicates that they were less abundant or available than Atlantic salmon, whitefish, and lake herring, and they apparently were less preferred than Atlantic salmon and whitefish (Smith 1894). Species of the percid and centrarchid families were referred to more frequently in the late 1800s after Atlantic salmon, whitefish, and lake trout had declined. They were sometimes called “cheaper grades” that maintained the fishery (True 1887; Smith 1892; Cobb 1898). Therefore, these three species were considered common or abundant but less valuable.

A survey of the United States fishery of Lake Ontario in 1885 showed that the total capital invested in the fishery increased from \$54,050 in 1880 to \$135,749 in 1885-a 15 1% increase. This increased investment occurred even though production declined from 8,025,000 kg to 5,288,000 kg-a 34% decline. Its value declined from \$159,700 to \$95,869-a 40% decrease (Smith and Snell 1891). These changes indicate that fishing had become increasingly unprofitable-despite greater investments to maintain the catch as stocks declined. Fishermen from Canada had stopped fishing on the south shore,-which was previously more profitable because of the closer proximity to United States markets. As a result, fishing effort was transferred from the United States to Canada where stocks had been less heavily exploited (Smiley 1882; True 1887).

The intense exploitation of the early and mid-1800s probably had a major influence on the fish stocks of the lake. A review of the fishery for 1890 (Smith 1894) concluded that there seemed “little ground for doubt that the lake has been overfished.” As fish stocks declined in Lake Ontario, fishermen turned to other professions or moved to other lakes. Even with greatly reduced fishing effort, the fish stocks failed to recover

to their former abundance. This failure to recover indicated that factors other than fishing may have been involved in the declines. As inferred by Smith and Snell (1891):

fishing as a means of livelihood along the shores of the great lake [Lake Ontario] . . . is rapidly decaying . . . once lively towns became dead and musty nets rotted on drying wheels

Drainage Modification

Cutting of forests and development of agricultural land during the period of colonization caused major changes in the hydrology of the Lake Ontario drainage. Of great value in themselves, the virgin forests were described by Hedrick (1933) as:

So thick set with trees and so dense were the boughs and leafage that a savage [American Indian] might skulk from the Hudson [River] to Lake Erie without exposing himself to the glare of the sun.

The forests, however, inhibited the use of land for agriculture. Therefore, forest removal was the major early activity in the Lake Ontario drainage:

- the trees produced lumber, fuel, tanners' bark, charcoal, and ashes for potash and fertilizer; and
- cleared areas provided good soil for farmland.

Although settlement of the region was progressing rapidly, the forests of the Lake Ontario drainage were described as "unbroken" in 1784 (Jones 185 1). The process of forest cutting progressed from east to west; by the 1890s, the drainage area of Lake Ontario in western New York was described by Rafter (1897) as "almost entirely deforested." Concurrent with the removal of forests was the drainage of swamps to create farmland and the construction of dams for water-powered mills. The construction of mills to process forest and farm products started in the late 1700s. By 1845, there were 7,406 sawmills run by water power in the state of New York (Hedrick 1933) and a somewhat lesser number of grist mills, plaster mills, tanneries, and other water-powered industries on both the United States and Canadian sides of Lake Ontario (Jones 1851; Anonymous 1866; McCombie 1968; Christie 1973).

These changes had a major influence on streams (Fig. 2). Initially the effect of forest removal on stream flow was controversial (Rafter 1897); however, by the end of the 1800s stream flows were greatly reduced. Hedrick (1933) observed that thousands of water-powered mills were abandoned and that “creeks and rivers in which water hardly flows in dry summer give mute evidence that forests play an important hydrologic role.” Some tributaries that previously supported Atlantic salmon runs became dry or intermittent. Summer flows in rivers where juvenile salmon spent their early life became very low during dry periods and the magnitude of seasonal or short-term fluctuations in stream flow increased greatly (Smith 1892; Hedrick 1933; McCombie 1968). The consequences of such changes were to widen and flatten stream beds and increase the silt load during periods of heavy runoff. Springs that contributed to sustained flows throughout the year dried up (Trautman 1957), probably as a result of swamp drainage and loss of the forest floor that had retained water from melting snow and summer storms.

A second but more-acute effect of developments in stream drainage was the discharge of mill and manufacturing wastes into the streams powering the mills. These discharges resulted in heavy pollution of nearly all streams throughout the drainage by the mid-1800s (Anonymous 1866; Smith 1892). The problem of pollution from mill wastes diminished somewhat in the late 1800s because laws were passed to control pollution. Reduced stream flows caused closure of most water-powered mills that had been releasing waste into streams (Smith 1892; Rafter 1897).

Low stream flows, dams, and pollution greatly reduced the usefulness of streams for spawning runs of fish—some streams became completely unsuitable for aquatic life. Spawning runs of large numbers of many species of lake fish described during the period of early exploration in the 1600s and 1700s (Thwaites 1896) were scarcely mentioned in descriptions of fishery resources during the mid-to-late 1800s. Stream-spawning species of the facultative migrants that could spawn in either lake or stream (percids, centrarchids, catostomids, and sturgeon) were either greatly reduced or eliminated by the changed stream conditions. (Stream-spawning lake trout, lake whitefish, and lake herring were described in the upper Great Lakes, but they were apparently not prominent or lacking in Lake Ontario.) The loss of spawning and nursery areas in streams may have reduced fish productivity in the lake by causing a substantial reduction in the progeny of stream-spawning fish that contributed to lake-dwelling populations,

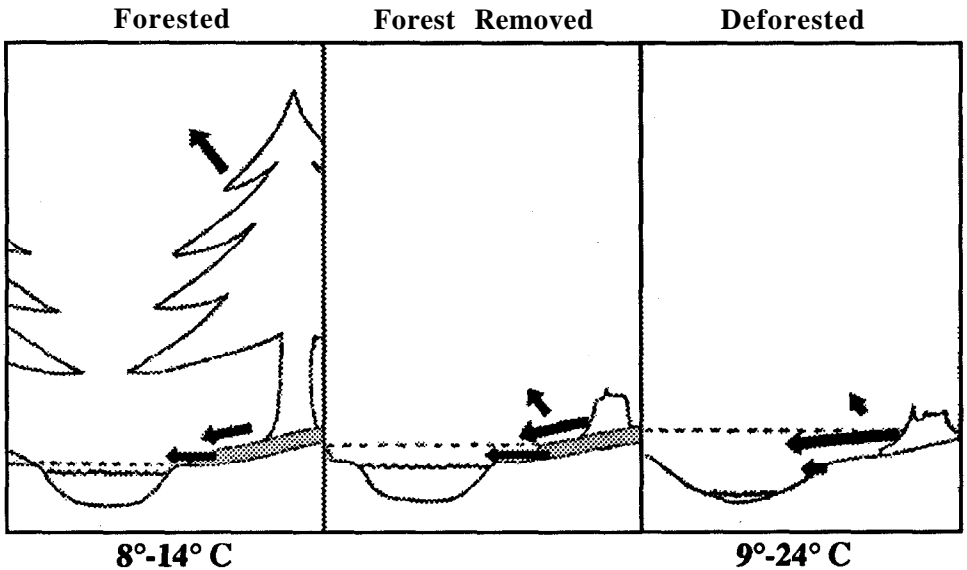


Fig. 2. A generalized representation of the effects of deforestation on stream bed, flow, and temperature. The arrows represent relative changes in amounts of water from surface runoff, soil seepage, and transpiration. Temperatures show maximum diurnal summer stream temperatures (Iwanaga and Hall 1973).

Loss of the Atlantic Salmon

The most-significant loss from changes in the tributaries was probably the Atlantic salmon—an obligate stream-spawning fish requiring a stream environment as a juvenile. The Atlantic salmon was greatly reduced by the mid- 1800s and considered extinct before 1900 (Huntsman 1944). Descriptions of the salmon runs in Fish Creek above Oneida Lake published in 1851 (Jones 1851) use the past tense—indicating that mill dams and pollution had probably blocked the run many years earlier. Similarly, a comment concerning Cayuga Lake published in 1866 (Anonymous 1866) stated:

Many of our citizens can well remember. . . the Salmon . . . [which] have been long shut out from this lake by the reckless manner in which its outlet has been dammed and its waters polluted with vile offal from Starch, Gas, and other Factories, located near the stream.

The decline of the Atlantic salmon and its eventual extinction from Lake Ontario received much attention (Anonymous 1874) because of its previous abundance and importance in the economy of the region. Abusive fishing-particularly with pound nets and trapnets at the mouths of spawning streams and with weirs in streams-was commonly acknowledged as the major factor for depletion. An exhaustive survey and review in 1890 (Smith 1892), when salmon had reached apparent extinction, surmised that “catching of salmon *per se*” *could* not have been the controlling cause and instead:

their decrease was due to the prevention of their ascent of the streams in sufficient numbers to secure the perpetuation of the species.

Factors cited by Smith (1892) as impeding or preventing spawning runs in addition to the fishery were:

- “insurmountable dams,”
- water “filthy with sewage and refuse from manufactories,”
- low stream flows that resulted from draining of “swamps that formerly acted as reservoirs for surface water,” and
- “the cutting away of the forests.”

A later, detailed review concluded “the presence of many dams and decreased flows in periods of drought provided a very poor background for the continuance of the salmon stock.” However, no conclusion about a cause for extinction was reached (Huntsman 1944).

All of these factors-recognized in the 1800s - as adversely affecting Atlantic salmon did not affect all streams. Some streams (Smith 1892) were described as:

- having adequate flows of unpolluted water,
- dams that salmon could bypass, or
- spawning areas that could be reached without obstructions.

Some streams were protected to prevent fishing (Huntsman 1944). In addition, Atlantic salmon were planted periodically from 1878 to 1970 in Lake Ontario tributaries-and in the other Great Lakes (Parsons 1973) - during periods after dams were gone and pollution was abated. However, none of the introductions resulted in the reestablishment of salmon runs.

A change not recognized in the 1800s may, therefore, have been the limiting factor that caused extinction of the Atlantic salmon and subsequently prevented reestablishment. Indeed, recent research has demonstrated that forest removal can cause marked increases in stream temperatures - with adverse effects on salmonids - as a result of greater heat input from solar radiation (Brown 1971; Brown, et al. 1971). Comparisons of salmonid streams in forested and deforested areas of Oregon in 1969, at the same latitude of the Lake Ontario basin, showed an average July-August temperature of:

- 11.0°C and diurnal fluctuation of 8.4°-13.7°C for a forested stream,
- 15.1°C and diurnal fluctuation of 9.2°-23.9°C for a stream where the forest was removed (Iwanaga and Hall 1973).

Other studies showed that forest removal could increase the monthly maximum temperature of a stream by 7.8°C, resulting in an annual maximum 15.6°C higher than for the same stream before forest removal (Brown and Krygier 1970).

Lake Ontario tributaries were described as clear and cool before the forests were cut, but no records can be found of stream temperatures during the period of forest removal. There is no question, however, that stream temperatures must have increased substantially following deforestation. The following is a typical description of undisturbed streams in the Great Lakes (Trautman 1957):

Stream banks were heavily wooded or covered with brush, which tended to make the stream narrow and deep. The trees overhanging the streams provided much shade, and there was considerable down timber and brush in streams.

The influence of solar radiation on stream temperature must have been minimal. After forest removal, and with it the great reduction of summer and fall flows and the broadening of stream channels from flooding (Smith 1892), solar radiation would have caused substantial and predictable increases in stream temperatures (Brown 1970).

The Atlantic salmon is a northern species, and the Lake Ontario drainage was at the southern extremity of its range in North America (Scott and Crossman 1973). It is characteristically found in cool streams where stream-resident juveniles appear to do best at approximately 12.8 °C (MacKay 1963). Also, the maximum food-conversion rate occurs at approximately 12.0°C (G. L. Rumsey, U.S. Fish and Wildlife Service, Cortland Field Station, 3075 Gracie Road, Cortland, NY, 13045-9357, pers. commun.), which usually closely approximates the preferred temperature of fish (T. Edsall, National Biological Survey, Great Lakes Center, 1451 Green Road, Ann Arbor, MI, 48105, pers. commun.).

Increased stream temperatures were not specifically mentioned in discussions of factors causing the decline of Atlantic salmon in Lake Ontario. However, a comment about the higher temperature tolerance of Pacific salmon (*Oncorhynchus* spp.), introduced to replace Atlantic salmon (Anonymous 1874), indicates that there may have been some recognition of temperature as a possible problem in the decline of the Atlantic salmon.

An intensive study was made of Atlantic salmon introductions from 1944 to 1947 in Duffin Creek (a tributary of Lake Ontario that was considered a better salmon stream) to determine why attempts to reestablish salmon had not been successful (McCrimmon 1950). The study showed that two major factors of mortality were:

- 1) lethal summer temperatures in the lower portions of the stream, and
- 2) inadequate protective cover in other sections.

Solar radiation was noted (McCrimmon 1954) as a major factor influencing stream temperature and:

Those tributary streams in which lethal summer temperatures destroyed the salmon populations . . . lacked any appreciable amount of shade, whereas those streams with suitable temperatures had a larger proportion of shaded sections.

Stream conditions other than temperature and cover were considered “of minor or no importance in salmon survival.”

A study of the Oswego watershed of Lake Ontario in the 1920s (Greeley 1928), which supported large runs of salmon prior to the mid- 1800s, showed that maximum stream temperatures ranged from **10.0°C** to **29.4°C**. This indicated that some areas would no longer be suitable habitat for Atlantic salmon. The report on the study commented that:

water, being exposed to the sun, has become too warm for trout The warmest streams contained many species of fish but were entirely avoided by the trouts.

These observations indicate that temperature conditions unfavorable for salmonids and the associated low flows persisted long after many other inimical factors associated with colonization and deforestation had ameliorated. Unfavorable stream temperatures, primarily as a result of forest removal, may have been a controlling factor leading to the extinction of the Atlantic salmon and prevented its reestablishment in the Lake Ontario drainage. Earlier contributing factors (exploitation, pollution, and stream barriers) were of shorter duration and have been eased greatly or eliminated by regulations and changes in commerce and industry. In addition to thermal change, low flows, scoured stream beds, and reduced shelter for fish have persisted to varying degrees and may have caused diminution or disappearance of migrations of the many facultative stream-spawning species.

Invasion of Marine Species

Loss of the Atlantic salmon and related environmental modifications were apparently the triggering mechanisms that started a sequence of changes in fish stocks that spread throughout the Great Lakes. The first two events (and perhaps most significant) that accompanied the disappearance of Atlantic salmon were the establishment of major populations of alewives and sea lampreys in Lake Ontario. Both were anadromous species that were very abundant in the coastal areas of the Atlantic Ocean east of Lake Ontario and were capable of completing their life cycle entirely in fresh water. Both species had unobstructed access to Lake Ontario from the northeast through the St. Lawrence River, which enters the Atlantic Ocean near the northern extremity of the range of each species (Scott and Crossman 1973). Descriptions of the fisheries or fish populations do not provide evidence that either species was very abundant at the mouth of the St. Lawrence River or had entered Lake Ontario in significant numbers by that route.

Alewife

The alewife was the first marine invader to become conspicuously established in Lake Ontario and eventually achieve a dominant role among the fish populations (Smith 1892). Alewives were recorded in the lower St. Lawrence River in 1863 (Evermann and Kendall 1902). The first record of alewives in Lake Ontario was in 1873 when three observers reported that they were present in abundance (Bean 1884). This indicated that they must have become established in the lake by the mid-to-late 1860s (Smith 1970). Alewife fry were apparently introduced with 5,000 American shad (*Alosa sapidissima*) fry released in Lake Ontario in 1870 (Smith 1892). However, the number of alewives among the 80,000 shad fry released in Lake Ontario between 1870 and 1872 was insufficient to result in the large quantities observed in the spring of 1873 (Smith 1970). Entrance by migration up the St. Lawrence River would seem more likely. However, migration is not supported by evidence of alewives in the long stretch of more than 483 km of river above the city of Quebec where alewives were described as absent or not abundant as late as 1878 (Bean 1884).

Although some alewives may have reached Lake Ontario via these routes, the alewives that appeared in abundance in the lake in 1873 probably entered the Lake Ontario drainage through the Erie Canal (Eaton 1928). This canal, constructed between 1817 and 1825 (Hatcher 1945), connected the Mohawk and Hudson Rivers (which entered the Atlantic Ocean where alewives were extremely abundant) with the Oswego River drainage in the Lake Ontario basin (Fig. 1). Alewives apparently had difficulty negotiating the locks and water-control structures of the canal because alewives were not reported in the Oswego River drainage until 1869. In 1869, they were described as abundant in Seneca and Cayuga Lakes and the river and canal below them (Smith 1970). This was the earliest record of alewives in the Lake Ontario basin. From this location, the Oswego River would have carried large numbers of alewives downstream into Lake Ontario during the 1860s. This source could easily account for the large numbers observed in Lake Ontario in 1873.

Speculation existed that alewives may have occurred as glacial relicts in small lakes in the Lake Ontario drainage (Toner 1934; Radforth 1944). However, this possibility remains uncertain because the records do not predate the establishment associated with the Erie Canal, and alewives in these lakes were presumed to originate from Lake Ontario populations (Scott and Crossman 1973).

The reason why alewives may not have become established in Lake Ontario earlier via the St. Lawrence River became apparent from observations of the alewife invasion into the upper Great Lakes. In each of the Great Lakes, an abundance of large piscivores delayed the establishment or influenced the abundance of the alewife (Smith 1970). Therefore, the large populations of Atlantic salmon in Lake Ontario and the St. Lawrence River could have been a strong deterrent for the movement of alewives up the long section of the river to Lake Ontario.

Once alewives become established in a large, deep freshwater lake in the absence of a large population of piscivores, they increase rapidly and become the most-abundant species in the lake in less than two decades (Smith 1970). As the alewife population increases, it greatly modifies the composition and abundance of zooplankton (Brooks and Dodson 1965; Wells 1970). The initial population increase culminates in a period when the alewife overpopulates the lake-resulting in major changes in growth, condition, and age structure of the population (Brown 1971). At high population density, alewives suffer mass mortalities from cumulative stresses (Colby 1971), but they continue to be the dominant species of the lake. Such a swift and extreme increase in a species to dominant abundance and biomass, and the change in the zooplankton of a lake, would logically result in major changes in the native-fish community of a lake.

Although not documented by scientific studies during the 1800s, early accounts of the alewife in Lake Ontario were well described. Bean (1884) and Smith (1892) reported:

- an increase in alewife abundance,
- suspected depletion of planktonic food,
- change in size and condition of alewives, and
- stresses leading to mass mortalities and effects on native species.

Large shoals of alewives were reported in 1873 and immense quantities in 1878 (Bean 1884). By 1890, the alewife had become “the most abundant fish occurring in Lake Ontario” (Smith 1892). After alewives became the dominant fish in Lake Ontario, Smith (1892) observed that:

Lack of food must no doubt be the principal if not the only cause of the excessive leanness which is universally recognized and commented on by fishermen many of whom state that a fat alewife is now rarely seen, although during the earlier years the fish were quite oily.

The “enormous mortality” of alewives that occurred “during warm weather, especially during June and July” was described, and fungus disease, deficient food, storms, and water temperatures were discussed as possible contributing factors (Smith 1892). In 1878, Bean (1884) considered the abundance of alewives to be a blessing because:

They supply all our edible fish with an abundance of food . . . [and that] . . . bass, trout, pike, pickerel and muskellunge . . . , are more plentiful than for many years past.

In 1880, walleyes had increased in size and their “great fattness” was attributed to the alewife (Smith 1892). There was, however, speculation (Mather 1881) about a relation between increase in the abundance of the alewife and the “extermination of the lake herring”-which was considered by Rathbun and Wakeham (1897) to have been “one of the most abundant fishes of this lake”-and the sharp decline of whitefish (True 1887; Smith 1892). Some people speculated that the alewife might become a valuable fish for humans as well as for piscivores. In addition, because of their great abundance, alewives might be a more-valuable resource than the fish they displaced (Mather 1881; Bean 1884). This change did not happen, however, and the reduction of alewives for oil became unprofitable because their oil content decreased after they reached maximum abundance (Smith 1892). Even the piscivores, which seemed to be favored during the increase of the alewife, declined after alewives became very abundant (Cobb 1898).

Changes in populations of native species observed in Lake Ontario during the increase and dominance of the alewife were verified by similar changes in Lakes Huron and Michigan-where the alewife also became the dominant species in the 1960s (Smith 1970; Aron and Smith 1971; Wells and McLain 1973). The general sequence of declines has been:

- Obligate shallow-water planktivores decline-the largest species first. Lake herring and emerald shiners were the most-abundant and conspicuous species influenced.

- Inshore stocks of facultative planktivore-piscivores decline at the height of alewife population density following an apparent initial increase that may be related to the greater availability of food supplied by alewives. Yellow perch and rainbow smelt (*Osmerus mordax*) were more conspicuously involved in the upper Great Lakes, but larger percids (*Sizostedion* spp.), centrarchids (*Micropterus* spp.), and pike (*Esox* spp.) were frequently mentioned in Lake Ontario,
- All species of deepwater ciscoes and the deepwater sculpin decline when the alewife becomes the most-abundant species in the lake. The slimy sculpin and spottail shiner, which live at intermediate and moderately shallow depths, are apparently little influenced by the alewife. The deepwater sculpin and smelt appear to recover to near-normal abundance after the alewife population subsides. Lake herring and emerald shiner show the least capability to recover, but they continue to be present at reduced abundance.

The suspected mechanism by which the alewife dominates other species is food competition. The ability of the alewife to greatly reduce or eliminate all large plankton from a lake may deprive larger species of fish of the larger plankton that may be essential for their survival (Brooks 1968). Alewives also eat larval lake whitefish (Hoagman 1974), feed heavily on their own larvae (Webb and McComish 1974), and may feed on larvae of other species (Smith 1970). Larval fish are, in fact, large planktoners and are the favored food of alewives (Brooks 1968). Alewives would be expected to have a feeding preference for the fish larvae that are present where alewives are abundant.

Possible influences of the alewife on larger native species in Lakes Michigan and Huron were complicated by the destruction of the larger species of fish by the sea lamprey-which reached these lakes and became abundant before the alewife. In contrast, the sea lamprey apparently did not become established in Lake Ontario until after the alewife had dominated the lake and was a suspected contributor to the declines of whitefish and lake trout (Smith 1892).

Sea Lamprey

The most conspicuous change in fish communities of the Great Lakes accompanied the invasion and establishment of the sea lamprey-an event for which the causative factors have not yet been fully understood or explained. The parasitic sea lamprey has proven to be highly destructive of larger native species when it becomes established in the confines of a lake.

The sea lamprey or evidence of its attack on fish was not mentioned in exhaustive discussion about the possible causes of the decline of fish stocks in Lake Ontario between 1850 and 1890 (Smith 1892; Huntsman 1944). Wounds and scars are very conspicuous on fish that have survived an attack by a sea lamprey in freshwater-fish communities (Applegate 1951). These marks would probably not be missed by the many observers who were seeking explanations for the declines. Also, sea lampreys would have been conspicuous (even at low abundance) and seen where their spawning runs were blocked by mill dams. If present, sea lampreys would have been included as a food source for humans because they were considered a delicacy by western Europeans (Gage 1928). These western Europeans made up a major component of the immigrants who colonized the Lake Ontario basin. Sea lampreys were also a well-known food item in North America and were much used as food by the people who colonized the northeastern coast of the United States (Goode 1884). If present, sea lampreys would have been taken in traps in streams that the native American Indians constructed to take American eels (*Anguilla rostrata*). These traps also took stream-migrant Atlantic salmon (Thwaites 1896).

Sea lampreys were not mentioned, however, in the descriptions of the fish and resources of Lake Ontario and the St. Lawrence drainage recorded in the extensive writings of Jesuit missionaries during 1610 and 1791 (Thwaites 1896). These observers had a penchant to notice the macabre, and a parasitic sea lamprey attached to a fish or the ugly wounds left on fish that survive an attack would have had a high probability of attracting their attention. The only use of the word “lamprey” by Jesuits (Thwaites 1896) was in a list of food eaten by native American Indians in “New France”-which included the “Great River St. Lawrence” and the adjacent Atlantic coastal area:

As to fish, they catch in season, different kinds of Salmon, Seals, Pike, Carp [suckers], and Sturgeon of various sorts; Whitefish, Goldfish [yellow perch], Barbels [probably Gadidae], Eels, Lampreys, Smelt, Turtles and others.

The mention of marine and freshwater species indicates that this is a generalized statement applying to the Gulf of St. Lawrence and perhaps the Atlantic Coast, as well as the St. Lawrence River. The use of the term “lamprey” does not necessarily refer to the sea lamprey. It does confirm that lampreys were known and that sea lampreys would have been mentioned in descriptions of the fish and fisheries of Lake Ontario or the St. Lawrence River if they were abundant as a food source or if their attachment to or wounds on fish were observed.

The possibility that the sea lamprey may have been native in Lake Ontario and abundant in the early 1800s has been a subject of recent speculation. An Ohio naturalist, Dr. Jared P. Kirtland, supposedly expressed concern in 1851 about the danger of the sea lamprey moving from Lake Ontario to Lake Erie through the Welland Canal-which was opened to ship traffic in 1829 to bypass Niagara Falls (Christie 1973). The source document was an unsigned article titled "Piscatoriana - No. 1" that appeared on page 78 of *the Family Visitor*, Cleveland and Hudson, Ohio (Trautman 1949). The author of the article states, "I shall chiefly confine my remarks. . . [to]. . . the sports of rod and line." There is no mention of the sea lamprey in the article, but a "silver eel" is listed among the most-favored and abundant sport species along with "salmon, trout, black and rock bass . . ." taken by anglers in the St. Lawrence River and Lake Ontario. In a discussion of Lake Erie, the author apparently hopes that silver eels would be a new-favored recreational species established in Lake Erie:

No silver eels are found above the fall of Niagara, but it is believed that they will ultimately find their way through the Welland Canal locks, and become plenty here.

The silver eel mentioned in the above article must refer to the American eel which was called the silver eel (Cheney 1899; Leim and Scott 1966; Scott and Crossman 1973). It was very abundant and was considered a recreational species at that time in the St. Lawrence drainage below Niagara Falls. The silver eel mentioned in the article could not have been a sea lamprey as was interred by Christie (1973). The sea lamprey was not known to be taken recreationally on "rod and line" like salmon, trout, black and rock bass, and it was never mentioned in discussions of either recreational or food fishes in extensive descriptions of the St. Lawrence drainage.

The Family Visitor article mentioned Prof. Kirtland among the list of devoted sport anglers and had the notation "Cleve. Her." at the end. Indeed, *the Evening Herald* of Cleveland had previously printed the identical article (probably the original article) on page 3 of the June 24, 1851, issue and gave the initials "D. W." at the end. Therefore, Dr. Kirtland was probably not the author of the article that did refer to "the earnest solicitation of a learned friend" who could have been Dr. Kirtland. Possible confusion may have resulted in the interpretation of this article by recent authors because the American eel was known as the silver eel, a name that could have been confounded with the silver lamprey (eel) described by Dr. Kirtland as *Petromyzon argenteus* in 1840.

P. argenteus was more abundant in the Great Lakes in the late 1800s and early 1900s than in recent years. It was not a species taken by rod and line, however, and its parasitism was not considered a substantial threat of major concern to fish of the Great Lakes.

Another reference (Christie 1974) that has caused speculation about the sea lamprey being endemic to the Great Lakes was its provisional inclusion in the fishes of Georgian Bay, Lake Huron, published in 1915 (Bensley 1915). This provisional record states:

Though there is no reliable information as to the occurrence of lake lampreys [*Petromyzon marinus unicolor*, a contemporary name used for landlocked forms of the sea lamprey], and the whitefish and trout are practically free from lamprey marks, fishermen state that lampreys about 15 inches (38 cm) in length are sometimes taken on whitefish and trout from deepwater.

The author assumed that the lampreys observed by the fishermen were sea lampreys-rather than silver lampreys (*Ichthyomyzon unicuspis*) - which were common in Georgian Bay. According to his information, the silver lamprey did not grow to 38 cm in length, and they fed primarily on “pike and garpike.” The Bensley collections were primarily from stream and inshore areas where these species would be common. Silver lampreys do measure 38 cm long in the Great Lakes (Trautman 1957), however, and do feed on whitefish and lake trout (Scott and Crossman 1973). Also, if the sea lamprey was a native species in Georgian Bay prior to 1915, and reached that area directly by possible post-glacial or recent routes (Radforth 1944):

- its sequence of dispersal in the upper Great Lakes should have been earlier, and
- it should have extended its distribution to other lakes from Lake Huron instead of the well-documented dispersal from Lake Erie-where it first appeared in 1921 associated with entrance via the Welland Canal (Applegate 1950; Smith 1971).

A third report (Christie 1973) that has been cited as a basis for the sea lamprey being endemic in the Great Lakes was the inclusion of the lamprey eel in “a list of fishes of the Toronto region in the *Handbook of Toronto* published in 1858. The *Handbook of Toronto* had the entry (Anonymous 1858):

The lamprey eel . . . *Petromyzon*. This fish is common in the lake where it is a parasite on the Salmon.

This report was most likely another instance where the sea lamprey was confused with the silver lamprey, which was known in the Great Lakes during the 1800s (Mimer 1874). The silver lamprey was placed *in the* genus *Petromyzon* by various authors between 1841 and 1886 (Scott and Crossman 1973). It is parasitic to fish but has never been known to be as abundant or as voracious a predator on lake fish as the sea lamprey has been.

Confusion of the identity of silver lampreys with sea lampreys continued even after the sea lamprey became established in the Great Lakes. Scott and Crossman (1973) state:

It [sea lamprey] was also at times confused with the other common lamprey in Lake Ontario, the silver lamprey *Ichthyomyzon unicuspis*. Wright (1892) illustrated a sea lamprey buccal funnel, called the specimen *P. concolor* (a synonym of *unicuspis*), gave it the common name silver lamprey, and seemed at times to be describing both species.

Therefore, the listing of “The Lamprey Eel . . . *Petromyzon*” in 1851, interpreted as a sea lamprey and common in Lake Ontario, must be assumed to be a misinterpretation in view of the overwhelming evidence to the contrary because of the lack of mention of the sea lamprey in extensive discussions of the fish, fisheries, and fish problems of Lake Ontario during the 1800s, and earlier.

The *Handbook of Toronto* (Anonymous 1858) demonstrates a clear recognition of the difference in the use of the name “silver eel” applied to the American eel and the lamprey. The book has the entry “Great Lakes Eel . . . *Anguilla*,” followed by the entries “Silver Eel” and “Longnosed Eel” (synonyms of what later become known as the American eel) preceding the entry and comment about “The Lamprey Eel . . . *Petromyzon*.”

The first positive description of a sea lamprey in the Lake Ontario drainage was made in Duffin Creek, a tributary of Lake Ontario east of Toronto, in May 1835, by Charles Fothergill (Lark 1973). He was a newspaper writer, artist, and naturalist with a particular interest in birds (Baillie 1944). This record is confusing, however, because it opens with, “This troublesome, formidable and destructive fish is but too common in Canada....” It further states that it is a threat to earthen mill dams because “they are fond of burying themselves in mud” in the winter and “will penetrate far into the banks of streams” The account also says:

Like the common eel [*Anguilla*] they not infrequently leave the water and crawl on shore-going to a considerable distance from the water-and it is equally tenacious of life.

Following these brief introductory comments, the record continues with a precise and accurate description of the color and morphology of the sea lamprey that was taken from Duffin Creek.

This record is confusing because Fothergill was known to be an astute naturalist. However, all records in North America and Europe-earlier, contemporary, and later than his description-give no indication that the sea lamprey:

- was considered a troublesome or destructive fish although it was considered (Goode 1884) semiparasitic by some, and suspected as being destructive “of food fish that enter estuaries and rivers;”
- was not common in Canada in the early 1800s except possibly in the southeastern Maritime Provinces (Cox 1893);
- was not mentioned as a threat to earthen mill dams;
- did not bury itself in mud or penetrate far into stream banks (as adults to which Fothergill’s record referred-larval lampreys that make shallow penetrations in mud were considered a different genera in the early 1800s);
- did not leave the water voluntarily like the common eel or go far from water; and
- was never called as “tenacious to life” as the American eel.

That Fothergill was a very keen observer is verified by his meticulous description of the morphology of the sea lamprey that he found in Duffin Creek. Therefore, it seems inconceivable that he could have so badly garbled an account of sea lamprey ecology if it had actually been based on his personal observations.

At the end of his remarks about lamprey ecology, Fothergill commented that he had no work of ichthyology “at hand” and wondered “how far the Canadian species differs from that of England.” Fothergill was educated in England and lived there before he moved to Canada at the age of 34 (Baillie 1944) - 19 years before he described the sea lamprey from Duffin Creek. Morphological descriptions of animals in the 1800s

frequently had added comments about ecology that were not first-hand information. Fothergill was apparently relying on his earlier readings of ichthyology in England, and what he may have read and heard in North America. Comparison of Fothergill's comments with an early British ichthyology text (similar to that which he might have read before coming to North America) suggests that he was confounding the sea lamprey with the European (or American) eel (Table 1). Indeed, a contemporary British ichthyology text (Hamilton 1843) stated that lampreys "resemble eels [*Anguilla*] . . . in the shape of the body, and . . . some of their habits." Only with respect to *Anguilla* does the text mention voraciousness and destructiveness. They bury themselves in mud in the winter, "voluntarily leave water, and travel over considerable space of land" and "their tenacity to life is well known" Fothergill repeated "tenacious of life" again at the conclusion of his morphological description. He may, in fact, have observed that the sea lamprey was much more hardy when held out of water than were other fish he had observed.

Table 1. Comparison of comments on the ecology of the sea lamprey and eel from three sources: a description from Lake Ontario in 1835, a British ichthyology text from early 1890, and early and recent descriptions in North America.

Lake Ontario-1 835' Sea lamprey	British ichthyology ² Sea lamprey	European eel
<p>“This troublesome-formidable and most destructive fish is but too common in Canada, at least for the security of such Mill dams as are constructed chiefly of earth.”</p>	<p>“This, the most conspicuous and best known member of the family [petromyzontidae], bears some resemblance . . . to the Muraena [Apodes] . . . It is frequently found in all the principal rivers . . . and has a very wide range throughout Europe and North America . . . They feed on almost any animal matter. . . and occasionally attack other fishes . . .” [No indication of concern about problems or destructiveness.]</p>	<p>“It is found in fresh waters of this country [Great Britain]; abounds throughout Europe occurs also... in North America.”</p>
<p>“In winter, they are fond of burying themselves in mud and will penetrate far into the banks of the streams they frequent.”</p>	<p>“It is a migratory fish, residing in the ocean during the winter months and ascending rivers in spring. ” [Adult life in the ocean was unknown. “It burries itself in the mud . . .” mentioned in describing the genus ‘ammocetes’ which were not then recognized as larvae of sea lampreys.]</p>	<p>“ . . . they are so voracious as to destroy all other kinds of fish . . .”</p>
<p>“Like the common eel too they not unfrequently leave the water and crawl on shore-going to a considerable distance from the water-and it is equally tenacious of life.</p>	<p>“The species [of Petromyzontidae] resemble [European] eels in relation to some of their habits.” [No mention of leaving water or that it was a hardy animal.]</p>	<p>“During the winter months they commonly bury themselves in sludge . . .”</p>
		<p>“Their tenacity to life is well known . . . They are able to remain out of water longer than most other fishes they often voluntarily leave the water, and travel over a considerable space of land . . .”</p>

¹ Transcription from the field notebook of Charles Fothergill (Lark 1973).

² Hamilton (1843).

Table 1 (continued)

Sea lamprey	Contemporary and recent information-North America American eel
<p>There was no mention of sea lamprey in the St. Lawrence drainage in extensive writings since 1610. Sea lamprey were mentioned as a very-abundant and valuable food source in the northeastern United States. Lampreys were reported attached to many species of fish in the marine environment on the Atlantic Coast south of the Gulf of St. Lawrence, but no prominent concern for destructiveness. There was no mention of problems at mill dams where adult sea lampreys would have been conspicuous during spawning migration.</p>	<p>American eel were frequently mentioned in accounts of the St. Lawrence River as a very-abundant source of food for native American Indians and early settlers. American eels were described as voracious and destructive carnivores. American eels were mentioned as a problem at water-powered mills in New York when they clogged machinery during their fall migration to the ocean.</p>
<p>Adult sea lampreys do not burrow. Sea lamprey ammocoetes reside in burrows throughout their larval life (all seasons), which are less than 150-mm deep in a soft substrate-mud, silt, or sand-and never in stream banks or compacted materials such as earthen mill dams.</p>	<p>Winter burrowing habits were well known. American eels burrowed randomly far into mud and stream banks.</p>
<p>There was no mention of sea lampreys out of water or on land, but they can move through crevices in low falls or openings in obstructions where water is flowing. Sea lampreys are incapable of directional movement when placed on land. They are quite hardy to handling, but when they are taken out of water have not been noted for "tenacity to life."</p>	<p>The habit of American eel to leave water and move considerable distances on land is known.</p>

American eels were common in the St. Lawrence drainage and along the Atlantic coast. They were considered to have “destructive qualities” and cause problems in the operation of water-powered mills (Cheney 1899). Sea lampreys were particularly abundant in streams of the northeastern United States. Therefore, Fothergill must have seen records or heard about American eels and sea lampreys on this continent. Indeed, Fothergill wrote a nature column for a newspaper after 1822 for which “most items [were] culled from English and United States papers” (Baillie 1944). Confounding the Atlantic eel and the sea lamprey gives little credence to Fothergill’s comment, “This troublesome, formidable and destructive fish is but too common in Canada” This comment is also negated because it is without confirming evidence, which would have been certain if the statement had a substantive basis. The description of a sea lamprey in Lake Ontario in 1835 is of particular importance, however, because it confirms that a sea lamprey had, in fact, entered the lake by way of the St. Lawrence River (or possibly the Erie Canal). However, the failure to establish a population of sea lampreys in the lake prior to the late 1800s must have special ecological significance.

The first major populations of sea lampreys in the Lake Ontario drainage were in the Finger Lakes (Cayuga, Oneida, and Seneca). They were abundant in Cayuga Lake as early as 1875 (Gage 1928) and were believed to have been in these lakes during the centuries after the glaciers had retreated. The sea lamprey probably entered by way of the St. Lawrence Valley after the ice block retreated or through the Hudson-Champlain estuary (Wigley 1959). If sea lampreys entered by these routes and were in the Finger Lakes for centuries, then they also would have been in Lake Ontario where a preponderance of early evidence indicates that they were inconspicuous or absent. Indeed, early information from the Finger Lakes indicates that the sea lamprey was probably not present or abundant in these waters prior to the mid- 1800s.

Descriptions of fish communities in Cayuga and Seneca Lakes in the early and mid- 1800s indicate that there were abundant populations of species that did not thrive or coexist with sea lampreys. In contrast, accounts in the late 1800s describe fish communities characteristic of lakes where landlocked populations of sea lampreys became established. An early account of fish in Cayuga Lake (Anonymous 1866) states:

The cold clear waters of this beautiful lake abound with valuable fish; Salmon-trout [lake trout], Whitefish [lake whitefish], Black-bass, Pike, Pickerel, Perch and Cisco’s [lake herring], are taken in great numbers.

Early accounts of sport fishing described the appearance and flavor of lake trout from Seneca and Cayuga Lakes in glowing terms (Herbert 1859; Scott 1869).

Subsequent experience when the sea lamprey became established in Lakes Huron, Michigan and Superior has verified that lake trout and lake whitefish were particularly vulnerable to sea lamprey predation. Lake trout stocks were greatly reduced and the remaining trout were heavily marked with wounds and scars from sea lamprey attacks-which gave them poor external appearance, pale flesh, and food quality. Whitefish were also greatly reduced where sea lamprey became abundant. Lake herring were attacked by sea lampreys (Dymond et al. 1929) and always declined when lampreys became established. However, exploitation and competition with alewife or smelt were usually involved when lake herring declines occurred.

When the sea lamprey was described as an abundant species in Cayuga and Seneca Lakes in 1875 and 1894, respectively (Gage 1928), lake trout, whitefish, and lake herring became minor species. There was much concern about the attacks of sea lampreys on these and other species. Proposals were made to control the sea lamprey (Gage 1893; Surface 1899) so these favored fish could be restored. (Intensive exploitation of these species for food and recreation would also have contributed to the reduction of stocks.) An account (Surface 1899) in the late 1800s states:

The lake trout is . . . very seriously attacked by lampreys. We rarely see a lake trout that did not bear two or more marks of this fish foe.

The incidence of lamprey wounds and scars in recent years was 84%-99% on lake trout in these lakes (Wigley 1959). Other species were commonly attacked by sea lampreys and more than half of such populations were wounded or scarred (Gage 1928). If the sea lamprey had, in fact, been an established native species in Cayuga or Seneca Lakes, some mention in the early 1800s of damage to fish rather than descriptions of the "unequivocally admirable" lake trout (Herbert 1859) would have been certain.

The evidence gives strong support to the assumption that the sea lamprey entered the Lake Ontario drainage by way of the Erie Canal from the Mohawk-Hudson River drainage-which enters the region of the Atlantic coast where sea lampreys were historically very abundant. Even though the abundance of sea lampreys in Cayuga Lake in 1875 occurred later than the abundance of alewives in 1868, the sea lamprey may have entered the Lake Ontario drainage through the Erie Canal earlier than the alewife. Sea lampreys commonly attach themselves to the hulls and rudders of boats (Gage 1928; Dymond et al. 1929), which would facilitate passage of sea lampreys

through canal locks (Great Lakes Fishery Commission 1956; Pearson 1957). Therefore, locks were less of an impediment for upstream movement of the sea lamprey than for a free-swimming fish such as the alewife.

Because sea lampreys require from 3 to 10 years or more to reach maturity (Smith et al. 1974), a longer period was required for them to become established in abundance compared to the alewife, which matures in 2 to 4 years (Brown 1972). Sea lampreys may have crossed the short section of canal between Utica and Rome (New York) linking the Atlantic and Lake Ontario drainages. That section was first opened to barge traffic in 1819 (Hatcher 1945). The sea lamprey then became established in Oneida Lake (where it is abundant today) during the next two decades. Sufficient numbers of lamprey facilitated subsequent dispersal westward through the canal system to Cayuga Lake-where they probably entered by the late 1850s or early 1860s in order to establish a thriving population by 1875. Establishment by this route and sequence could also account for a possible origin of the single sea lamprey taken in Duffin Creek in Lake Ontario in 1835. It could have been an adult derived from an ammocoete that migrated down the Oswego River from Oneida Lake. Its length of 45.7 cm is the size that sea lampreys attain maturity in fresh water when their abundance is low and food is plentiful (Smith 1971).

The sequence of sea lamprey establishment in the Finger Lakes through the Erie Canal agrees with the timing that would lead to the early reports of an abundance of sea lampreys and of fish wounded or killed by lamprey attacks in Lake Ontario during the late 1880s and 1890s (Dymond et al. 1929). Approximately 15 to 20 years were required after the first sea lamprey appearance for the development of major populations of sea lampreys in Lakes Michigan and Huron (Smith 1973), which are large lake systems comparable to Lake Ontario. Sea lampreys that were needed to start the population in Lake Ontario must have been entering the lake during the 1860s. This sequence coincides with the period of dispersal from Oneida Lake through the Erie Canal and Seneca-Oneida River systems to Cayuga Lake-all of which drain into Lake Ontario through the Oswego River (Fig. 1).

Because metamorphosed larval sea lamprey migrate downstream until they reach a large body of water, and adults do not migrate downstream during their life cycle, few adults from the Oneida Lake population would have moved into Lake Ontario. The most expeditious method of dispersal in a canal system would more likely be by adults clinging to boats. Because the majority of canal barges moved westward rather than down to Lake Ontario, the earlier dispersal to and colonization of Cayuga Lake would be expected.

Sea lampreys did not cause extinction or near extinction of lake trout in Lake Ontario and in Seneca and Cayuga Lakes as occurred in Lakes Huron and Michigan. This anomaly may, in part, be related to inhibited sea lamprey reproduction because of enriched stream conditions from wastes. Environmental degradation is believed to have made the tributaries of Lake Erie and southern Lakes Michigan and Huron less productive for sea lampreys than the more-northern streams where agricultural development and human population were sparser (Lawrie 1970). Also, mill dams may have continued to block spawning runs in some streams (Smith 1892), when sea lampreys were becoming established in the Lake Ontario drainage, and prevented rapid increase to maximum populations as occurred in the upper Great Lakes. In recent years, however, lake trout in Lake Ontario have not been able to survive to maturity, which has been attributed to sea lamprey predation (Christie 1973).

Lake trout in Cayuga Lake grow to maturity but do not reproduce and are maintained by stocking hatchery-reared fish, but in Seneca Lake they maintain themselves by natural reproduction. In Seneca and Cayuga Lakes, a lower sea lamprey abundance-to-prey biomass may exist because of the limited amount of sea lamprey spawning streams. This limitation, or other factors, must provide a degree of biological accommodation because lake trout survive to maturity even though virtually all of them bear multiple scars from lamprey attacks.

The general climatic cool period in the Northern Hemisphere from the late 1500s to 1900 could have suppressed sea lamprey reproduction. The sharp warming after 1920 (Bryson 1974) may have enhanced it throughout the Great Lakes drainage in recent decades. This climatic change could, in part, explain why lake trout did not become extinct in Lake Ontario and the Finger Lakes in the early part of this century, even though they have had greater difficulty surviving to maturity after sea lampreys became abundant in Lakes Superior, Michigan, Huron, and Ontario in recent years-prior to implementation of sea lamprey control.

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