## The American Eel: A Fish of Mystery and Sustenance for Humans

### Michael J. Miller and John M. Casselman

The American eel, *Anguilla rostrata*, is, in many ways, a typical anguillid in body shape and size and life cycle (Fig. 11.1), and also in that people who encountered it and needed sustenance always found it to be excellent food. It lives in watersheds adjacent to the Atlantic Ocean from the Caribbean Sea and Gulf of Mexico to Atlantic Canada (Fig. 11.2) and it has been caught and eaten by humans in all parts of its range at one time or another. The American eel has been important in the lives of many people historically and still is today, but its importance has been largely unnoticed by many. Probably as much as for any anguillid eel in the world, however, anthropogenic activities and particularly dam-building have reduced the area in which the species once lived (Fig. 11.2).

Native peoples and early colonial settlers along the entire east coast of North America knew the American eel to be an important source of sustenance and protein. Eels were valuable as food on both sides of the Atlantic far back in human history (Casselman 2003; and see other chapters in this book), but little else about them was certain. Then, early in the twentieth century, both American and European (Anguilla anguilla) eels became famous among biologists and the general public as much for their mystery as for their amazing migrations. For centuries, if not for millennia, humans wondered where the eels went to reproduce. Reproductive-stage silver eels would migrate out of lakes and rivers into the sea in autumn, when many of them were caught for food, but where they went to spawn remained unknown. Then, as surely as the seasons change, there would be a rush of young glass eels returning to swarm up the rivers and streams after

M.J. Miller (🖂)

J.M. Casselman

winter. These would then disappear into their watery world, rarely to be seen as they develop into silver eels. This was the life of eels as seen by humans, but what they did in the ocean was still unknown.

Then, in 1904, Johannes Schmidt and colleagues from Denmark collected the first leptocephalus (the technical term for an eel larva) of the European eel in the North Atlantic west of the Faroe Islands (Schmidt 1927). Catching that 77-mm long leptocephalus was significant, because there was a belief at the time that the European eel reproduced in the Mediterranean Sea, so its capture off the Faroes provided the first clue that these mysterious fish might spawn in the Atlantic. Its collection triggered an 18-year quest to find the birthplace of eels, a quest that extended to other species in other oceans (Schmidt 1935) and seemingly stimulated other scientists, including some studying the American eel, to search the oceans for eels. Schmidt collected leptocephali all over the North Atlantic, but the smallest leptocephali of both American and European eels were captured only in the southern Sargasso Sea; it was clear that both species must reproduce only there (Schmidt 1922).

This discovery that both European and American eels swam thousands of kilometres out into the ocean to reproduce seemingly brought these unglamorous, secretive fish to the attention of the world as never before. They were familiar to Native Americans in many parts of eastern North America because they provided more nourishment than many other fish (Casselman 2003). Others later used aboriginal methods of building weirs to catch downstream-migrating silver eels, and even today such weirs are still used in some places (Prosek 2010). Meanwhile, the story of the incredible migration of eels out into the ocean and the return of the larvae to where their parents had lived on two widely separated continents became a subject of huge interest to many scientists.

Other efforts were made to learn more about the spawning areas of American and European eels (McCleave 2003), and research into their biology in continental waters continued throughout the twentieth century. There was another change

Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwanoha, Kashiwa, Chiba 277-8564, Japan e-mail: miller@aori.u-tokyo.ac.jp

Department of Biology, Queen's University, 2406 Biosciences Complex, 116 Barrie Street, Kingston, ON, Canada K7L 3N6 e-mail: john.casselman@queensu.ca

in how people viewed the American eel when the numbers of glass eels or juveniles returning from the sea to freshwater suddenly declined, especially the numbers counted as they ascended eel ladders at dams on the St Lawrence River (Castonguay et al. 1994; Casselman et al. 1997a; Casselman

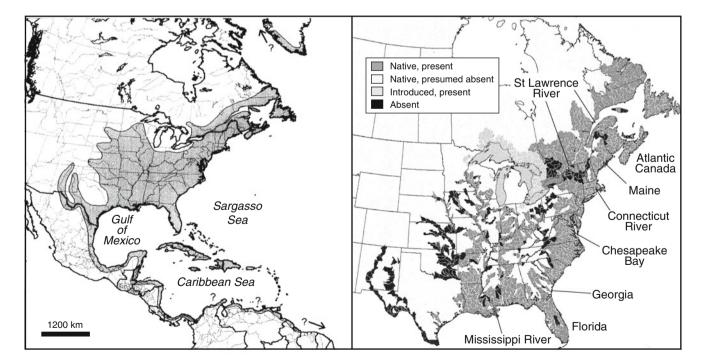


**Fig. 11.1** The American eel, *Anguilla rostrata*, at the yellow, natural silver and artificially matured silver eel stages (*top to bottom*). The larger eyes and darker body colouration are characteristics of silver eels migrating to their spawning area in the Sargasso Sea. Photograph courtesy A. J. Haro

2003). These dramatic declines of the once large eel stock of the upper St Lawrence River and Lake Ontario (Casselman et al. 1997b) and also the declines of European (Dekker 1998) and Japanese (*Anguilla japonica*) eels (Tsukamoto et al. 2009) prompted the holding of a scientific symposium specifically on anguillid eels in Québec, Canada, in 2003 (Casselman and Cairns 2009); scientists at that meeting publicly expressed their concern strongly (Dekker et al. 2003). Many reasons were proposed for the declines, but identification of the main reason remained elusive.

American eels traditionally moved up the large rivers far into the North American continent, but they were losing access or safe passage to vast areas of their former range (Fig. 11.2) as a result of dam construction for hydroelectric power or flood control (Haro et al. 2000). This reduced the habitat available to them, and even if the young eels could still climb over small blockages or use eel ladders constructed to help them, downstream-migrating silver eels experienced heavy mortality at the dams when attempting to return to sea (Haro et al. 2000; McCleave 2001).

The decline of eels in North America and the northern hemisphere generally began to become an increasingly interconnected global issue for humans because the Japanese eel was traditionally very important as food in East Asia, with demand greater than the supply from the wild. Intensively cultured, with wild-caught glass eels used as seedlings for producing market-sized eels (Tsukamoto et al. 2009), the



**Fig. 11.2** Maps showing the historical distribution range of American eels in North America (*left*), and the areas where they still remain through natural recruitment or stocking and where they are no longer

present because of blockages to upstream migration by dams (*right*). Adapted from USFWS (2007)

decline in recruitment of Japanese eels forced glass-eel traders to look to North America and Europe for another source of their seedlings. This resulted in a "goldrush" for glass eels in places such as the US state of Maine that still allowed glass eels to be fished (Facey and Van Den Avyle 1987; Prosek 2010). The price paid for glass eels soon rocketed, and guns were drawn as fighting ensued. In spring 2012, the price paid by distributors for glass eels reached an all-time high of US\$2,600 per pound, and during the 2013 season for glass eels, there were daily newspaper articles about rampant illegal fishing. Indeed, in a television documentary aired that year, individual fishers in Maine were stated to be making up to \$104,000 in a single night (Public Broadcasting System, PBS, documentary, The Mystery of Eels). Apparently too, on the opening night of the 2012 season, which had been on a Thursday, a local eel dealer paid >\$250,000 in cash and IOUs to local fishers for their catches of glass eels, and all the banks in coastal Maine ran out of cash and had to wait until the following Monday to receive more from Boston. The problem arose simply because glass eels from all over the world were being sought to support the extensive aquaculture industries in China, Japan, Taiwan and Korea (see other chapters in this book).

Unlike the Japanese eel, the American eel has not traditionally been very important as food for most Americans and Canadians, except for Aboriginals, so many of the silver eels historically caught in places such as Maine and the St Lawrence River system were shipped to Europe, where the tradition of consuming eels was stronger. Eels can be packed in high density and shipped live or frozen. However, that market declined around 1982 because of economic factors (Facey and Van Den Avyle 1987).

Scientists have long realized the ecological importance of the American eel and extensive research has been conducted on the species. Realization that its population was declining resulted in more dedicated research being carried out, new regulations being established to protect it, and systems to monitor its population being expanded (ASMFC 2012). Much of the research focused on determining how to facilitate glass eels ascending and silver eels descending past dams safely (Richkus and Dixon 2003). The decline in the population even triggered efforts to have the species declared as endangered in the US (USFWS 2007; Prosek 2010).

The American eel has played an important part in the lives of the people who share the rivers, lakes and streams with the species. It has inspired scientists to devote their whole lives to studying the species and to spend years at sea on research ships. Before being stopped by anthropogenically constructed barriers, the species travelled as far inland in the North American continent as any other anguillid eel on another continent. Despite being distributed from the Caribbean to Atlantic Canada, the American eel is known to be a single randomly mixing population (Wirth and Bernatchez 2003), so this chapter now looks briefly at some aspects of the relationships between American eels and the people who lived alongside them.

#### **Eels as Food in North America**

Casselman (2003) overviewed evidence of the importance of the American eel to Aboriginals in the St Lawrence River region of northeastern North America, and the evidence was revisited by MacGregor et al. (2012). Various tribes clearly used eels as a food resource. The St Lawrence River system extends far inland and includes many tributaries and Lake Ontario, and Junker-Andersen (1988) provided a unique ethnic and archaeological perspective on the lives of Iroquoians and their fisheries for eels there. Smoked eel was light in weight but nutritious, making it an important food for travellers (Casselman 2003). Indeed, it is likely that eel meat is more nutritious than that of most other fish, so it provided a valuable source of protein and helped people survive the long, cold winters (Casselman 2003). Large numbers of eels could be speared at night, using fire as a light source, in tributaries of Lake Ontario (Casselman 2003). Runs of migrating silver eels started in late summer or autumn, and these eels could be caught in large numbers in weirs constructed across streams or within large rivers, providing a valuable resource just before the onset of winter. Smoked, stored eels were used to prevent famine if other food was not available.

The extent to which American eels were used by other native peoples farther south, in warmer areas of the species' range, appears to be less well documented. An early woodcut from 1590 by Theodore de Bry shows the use of spears and weirs to catch fish, including eels, in Virginia (Fig. 11.3). It would be surprising, however, if eels were not being utilized as at least a seasonal food source by all the peoples who lived within their range. Indeed, in spring 1621, soon after the Pilgrims landed at Plymouth Rock in Massachusetts, there was a desperate need of food, and the first thing a local chief who decided to help them showed them was to catch and eat eels, probably saving them from starvation (Prosek 2010). For this reason, some have suggested that eels be made the symbol of the American Thanksgiving dinner rather than turkey!

Eels are still smoked and sold in some parts of the US, and eel is consumed in small quantities in Atlantic Canada (Fig. 11.4; Prosek 2010), but the eels of the east coast of North America are still not really a familiar or common food of modern Americans and Canadians. Perhaps many, especially those living outside Atlantic Canada and the eastern US, have never eaten eel, and some of those living along the coast may be more inclined to think of small eels less as food and more as bait for catching fish such as striped bass. **Fig. 11.3** Orr's (1917) reproduction of an engraving from 1590 by Theodore de Bry in Virginia showing the use of spears and weirs to catch fish including eels. Reproduced with permission from the Archives of Ontario, Toronto, Ontario

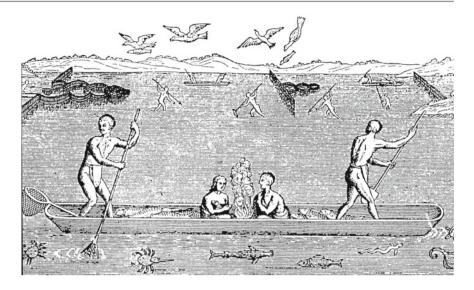




Fig. 11.4 Sliced and seasoned smoked eel packaged for sale (*left*) and a sign advertising the sale of eel and other fish in Québec, Canada. The listing of "anguille" for eel in French is referring to American eel

The small eels there are caught in eel pots in rivers or estuaries and sold to fishers as bait. Until recently too, many of the migrating silver eels captured in weirs in rivers and streams in out-of-the-way locations in Maine (Fig. 11.5b) and to the south were gathered by distributors who air-freighted them to markets in Europe and, more recently, Asia. Prosek (2010) provides examples of these weirs and the men who fish them, and the way one fisher catches silver eels in a weir (Fig. 11.5a) on the east branch of the Delaware River near Hancock, New York State, in the Catskill Mountains was also featured in the documentary on eels aired by PBS in their Nature series, *The Mystery of Eels*: throughout summer, the long stone walls of the weir are repaired while the water of the river is low, to prepare for the autumn downstream migration of silver eels. Most of the run is typically over a period of just a few nights during a new moon, when a storm in the catchment causes the river level to rise, and >1,000 eels can be caught in the weir in a single night, to be



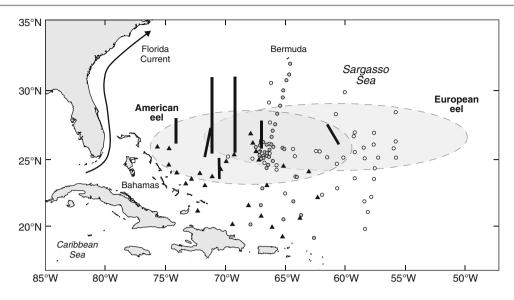
**Fig. 11.5** Examples of eel weirs used to collect silver eels of the American eel in recent years: (a) the eel weir built by a fisher on the East Branch of the Delaware River in the Catskill Mountains of New York that was featured in the recent book and documentary about eels (Prosek 2010; PBS documentary: *The Mystery of Eels*; photo courtesy

smoked and sold locally. To the north too, at the mouth of the St Lawrence, there was a long tradition of fishing huge tidal weirs that extended out from the edge of the river (Fig. 11.5c; Verreault et al. 2003), although typically those fishers were farmers trapping the large eels in autumn as an extra source of income.

More recently, young North Americans have become familiar with eels because of the greatly increased popularity of Japanese sushi restaurants. However, despite American eels being found along the whole east coast of North America, those consuming sushi with eels in North America are more likely to be eating American or European eels caught as glass eels in Maine or France, then shipped to China to be raised before being returned to North America for serving on sushi. J. Prosek), (**b**) an eel weir on the Seboeis River in Maine (photograph courtesy A. J. Haro), and (**c**) an eel weir on the St Lawrence River upstream of Québec City, Canada. The size of the weir can be seen relative to two pick-up trucks parked nearby. The eels are removed from the weir during low tide

#### **Spawning Areas**

It is difficult to know how the general public viewed the American eel during the first decades of the twentieth century when Johannes Schmidt's research expeditions discovered the spawning area of both American and European eels in the southern Sargasso Sea. Schmidt did perhaps envision the importance of knowing where eels were reproducing though, because he used many ships to collect the samples he needed to determine where European eels were spawning, including research vessels, ships of opportunity, particularly Danish commercial ones, and naval vessels (Boëtius and Harding 1985; McCleave 2003). Johannes Hjort, on board the steamer "Michael Sars" also caught small eel larvae in the



**Fig. 11.6** Map of the Sargasso Sea spawning area of American and European eels, showing the locations where tows of Isaacs–Kidd midwater trawls were made by American and German research teams between 1979 and 1989. Circles depict the German stations (Schoth and Tesch 1982, *white circles*; Tesch and Wegner 1990, *grey circles*), triangles the stations of Kleckner et al. (1983), and lines the transects of

Kleckner and McCleave (1988), except for the westernmost transect that was made during the 1989 expedition to locate and catch adult eels. The shaded ovals show where the smallest leptocephali of each species were collected (<6 mm long) during all cruises by Danish, German and American research teams up to 2007 (adapted from unpublished material of the first author and others)

central Atlantic, suggesting that the area where eels spawned might be far out in the Atlantic (Hjort 1910).

Much is written about Schmidt's life and work in the Danish chapter in this book, but to supplement that and to focus more on the American eel, further detail is given here. Schmidt initially used the schooner "Margrethe" to travel from Europe to the West Indies in 1913, and encountered both American and European eel leptocephali in some of the same tows of his sampling net (Boëtius and Harding 1985). However, later that year the "Margrethe" was wrecked on Anegada Island, British Virgin Islands, and with World War I intervening, no more collections of eel larvae were made until 1920 (Boëtius and Harding 1985). Schmidt then returned to the Sargasso Sea in 1920 in the motor schooner "Dana I," to the area where the smallest leptocephali had been collected before the war, and he caught many more between February and August (Schmidt 1922; Boëtius and Harding 1985). It was the data collected in those surveys that led to Schmidt's description of the spawning area of American and European eels (Schmidt 1922), but further collections were made by the "Dana I" from February to May 1921 and by the RS "Dana II" from April to June 1922, and these were consistent with the published conclusions about the spawning areas of the two species (Boëtius and Harding 1985; Kleckner and McCleave 1985; McCleave 2003). The implications of Schmidt's discovery for scientists and the general public were remarkable: both species were migrating thousands of kilometres through almost featureless ocean to the same small area of the North

Atlantic to spawn, but there was no understanding of how they could possibly achieve this. Equally remarkable from the standpoint of basic logic was how the small leptocephalus larvae that originated from almost the same area of the Sargasso Sea could return to their respective habitats in either North America or Europe without becoming totally mixed in each area.

Although Schmidt's work publicized both species of eel for their migrations each way, it was clear to scientists in both North America and Europe that there was much more to learn about the spawning areas of the two. All Schmidt's data plus other data on the American eel were then assembled and eventually published to provide the first perspective of what had been collected by Schmidt and others (Kleckner and McCleave 1985). The first American research expedition to the spawning area was led by James D. McCleave of the University of Maine in February 1981. That survey detected a temperature front and collected leptocephali along its southern edge (Kleckner et al. 1983; Fig. 11.6). Independently 2 years earlier, a German team led by Friedrich-Wilhelm Tesch had collected leptocephali over a much wider area. Tesch was well-known at the time for publishing his comprehensive work "The Eel" in 1977, and it was updated and reprinted in 2003 (Tesch 2003). The German expedition had hoped to collect eel larvae with plankton nets and adult spawning eels with a midwater trawl. They documented how American and European eel larvae were spread across the longitudes of the spawning area (Schoth and Tesch 1982), but no adult eels of either species were caught. The German



**Fig. 11.7** Cover photographs of the journals *Science News* (cover photograph made by the first author, reprinted with the permission of *Science News*) and *Nature* (cover photograph by N. Mochioka, permission granted by Nature Publishing Group) that included articles

about the American expedition to the Sargasso Sea spawning area to collect spawning adult American eels in 1989 and the discovery of the spawning area of the Japanese eel in 1991

team made a second expedition in 1981 to determine the latitudinal distribution of larvae (Tesch and Wegner 1990; Fig. 11.6), and the American team continued its research with cruises in 1983, 1984 (for large larvae), 1985 and 1989 (Fig. 11.6). The cruises in February and April 1983 and in March 1985 consisted of transects crossing the temperature fronts thought to influence the spawning locations of eels (Kleckner and McCleave 1988), and the catch data revealed that a northern front in the spawning area formed the northern limit of spawning (Kleckner and McCleave 1988). Finally, the collections of larvae by Schmidt and the German and American survey teams were combined to evaluate the overlap in the spawning areas of the two eel species based on the small leptocephali collected (McCleave et al. 1987; Fig. 11.6).

The most recent American expedition to the spawning area was made in 1989. Its goal was to use advanced fishfinder-type hydroacoustic systems to search for spawning aggregations of eels near the fronts and to attempt to capture them by trawl or in traps baited with artificially matured American eels. Many fish-like targets were seen on the echosounders that could have been eels, but not one eel was caught. The story of that cruise was published in Science News Magazine (Pennisi 1991), shortly after another cruise targeting eel larvae in the western North Pacific had succeeded in locating the spawning area of the Japanese eel (Tsukamoto 1992), a goal of Japanese scientists for decades. The story contrasted the outcomes of the two expeditions, one with massive effort to find and catch spawning adults that ended in disappointment, the other that succeeded well beyond expectations and which was symbolized by a cover photograph of a rainbow taken during the cruise in the Pacific (Fig. 11.7). Although the American survey was unsuccessful at catching any adult eels, another transect was made to collect larvae, and the data from that transect were combined with the catch data from other surveys to investigate the overall assemblages of leptocephali in the Sargasso Sea (Miller and McCleave 1994).

Despite these successes, however, it was another 20 years before scientists finally collected adult anguillids and their recently spawned eggs in the ocean; these were of the Japanese eel in the Pacific (Chow et al. 2009; Tsukamoto et al. 2011). In many ways, the quest by research teams from Denmark, Germany and the US to understand the reproductive ecology of the Atlantic eels, and the many research expeditions by Japanese scientists in the Pacific (Shinoda et al. 2011), represent a remarkable example of scientific resolve, perhaps to the point of obsession, to learn all there is to know about these mysterious fish. One part of the quest was that of Katsumi Tsukamoto of the Ocean Research Institute of the University of Tokyo, one of the editors of this book, who made many surveys that ultimately led to the collection of anguillid eel eggs for the first time on 22 May 2009 (Tsukamoto et al. 2011), 105 years to the day after Schmidt's collection of the first anguillid leptocephalus in the Atlantic Ocean on 22 May 1904. The research is continuing to this day, with a recent Danish survey to the Atlantic spawning area in 2007 (Munk et al. 2010) followed by a German survey in 2011; both teams are also planning surveys again in 2014. Surveys in the Pacific have now switched to attempting to observe spawning eels directly in the wild during New Moon periods, using submersibles and other underwater camera systems (Tsukamoto et al. 2013).

#### The American Eel in Rivers, Lakes and Estuaries

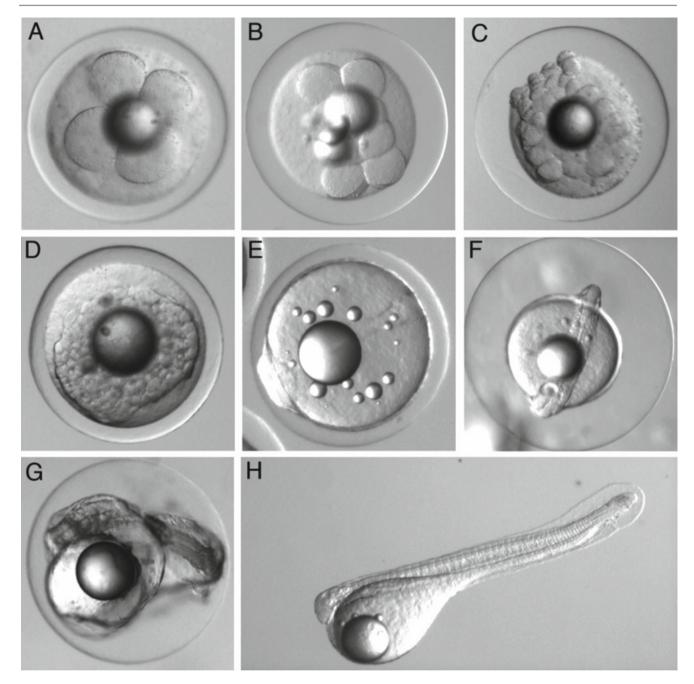
The life history of the American eel is similar to that of other anguillids, and many of the fascinating discoveries about eels have been made by those studying A. rostrata. It has the same life history stages of egg, pre-leptocephalus, leptocephalus, glass eel, yellow eel and silver eel as other species of eel, and its adult size is similar to that of most other species, though smaller than some of the tropical ones. Although its spawning migration is not as long as that of the European eel, its migration is still very long, much longer than that of some tropical eels. The American eel is also apparently good at keeping time, having what is known as a biological clock. The generally transparent glass eels enter estuaries (Haro and Krueger 1988), but most then must move upstream, which in large rivers can be difficult because of the outward flow. Studies on glass eels entering the Penobscot River estuary in Maine provide some of the best information about the mechanism of selective tidal stream transport used by eels and other fish. In large estuaries with strong tidal flow, such as the lower Penobscot, glass eels swim upstream during flood tides, using the flow to help them up the river (McCleave and Kleckner 1982). They also seemingly rest on the riverbed during ebb tides, and the timing of their movement off the riverbed is regulated by a biological clock related to the tidal/lunar cycle (Wippelhauser and McCleave 1988).

The young eels entering and moving up rivers are rarely seen, though, except by those who inspect small dams during spring and see the eel-like creatures slithering up wet areas and over the obstruction. Once the young eels find a place to settle and start feeding, their yellow eel juvenile growth stage begins, and then they are encountered only by those who catch them with a hook baited with a worm or minnow and leave them to lie on the bottom of a stream (Prosek 2010). An angler may at first mistake an eel for a large bass or another fish, because eels are able to swim strongly backwards, pulling the line very hard.

American eels emerge from their daylight hiding place at night to feed on aquatic insects, crustaceans, small molluscs, frogs and small fish (Facey and Van Den Avyle 1987), just like other eels in similar habitats. Research on the feeding behaviour of American eels has revealed that when they encounter food items too large to swallow, they grasp the food in their jaws and spin their bodies round and round rapidly to tear off a piece to swallow (Helfman and Clark 1986). This has been referred to as "rotational feeding," and smaller eels have been recorded spinning their bodies at rates of up to 14 turns per second! The time American eels spend feeding and growing as yellow eels before they start their migration back to sea can vary widely, from several years to decades, based on the habitat in which they live, the density of other eels present and the latitude (Oliveira 1999; Oliveira and McCleave 2000; Jessop 2010). In fact, the sex of each American eel and likely all other anguillids seems to be determined by the density of eels and the growth conditions (Krueger and Oliveira 1999). Male yellow eels mature younger than females, which also attain a larger size, and this is likely part of their reproductive strategy (Helfman et al. 1987). American yellow eels tend to find an area in which to live and feed without moving around much, i.e. a home range, and the use of electronic tags has confirmed that they do tend to stay in that range, be it a stream, pond or other habitat, including river mouths and estuaries. One study showed that yellow eels used selective tidal stream transport to move small distances up and down the lower Penobscot River to feed before returning to their daytime hiding place (Parker 1995).

As mentioned elsewhere in this book, it has been possible to determine from the strontium/calcium content of the otoliths (ear stones) of American eels whether an eel has lived in totally freshwater or in brackish water in an estuary. Many American eels that entered freshwater as glass eels and lived there for some time then returned to the estuary to finish their yellow stage, whereas others remained in the estuary seemingly without ever having entered freshwater (Jessop et al. 2008).

Anyone who has ever visited an eel weir on a river or stream such as those shown in Fig. 11.5a, b after a rainy night will carry away a feeling of the wonder of migrating eels for the rest of their lives. A surprising variety of sizes, shapes and colours of eels from anywhere upstream of the weir can all end up in the same catch box at the same time, despite having developed in very different habitats upstream. Some will have come from just upstream of the weir and some from hundreds of kilometres away, perhaps in a small stream or lake.



**Fig. 11.8** American eel eggs (embryos) obtained from artificially matured silver eels caught in the Sebasticook River, Maine, and held in the laboratory in Massachusetts (reproduced with permission from

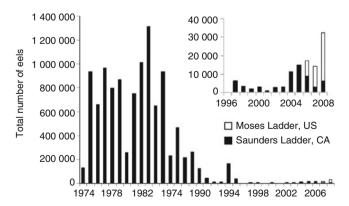
Oliveira and Hable 2010. See title and publication detail in References. © Canadian Science Publishing or its licensors)

Downstream migrations generally take place during autumn as temperatures fall and are usually complete before winter. American eels and other temperate anguillids tend to migrate downstream on rainy nights or during the dark phase of the lunar cycle (Haro 2003). Any master of an eel weir will report that few eels are caught on a clear night with a full moon even in the heart of the autumn migration, but if there is a big storm during the night of a full moon, introducing a lot of precipitation into rivers and streams in an area, more eels will be caught than during a clear night under a new moon. Some have recently unlocked parts of the secretive life history of the American eel by inducing silver eels to spawn eggs in the laboratory (Oliveira and Hable 2010). This was accomplished by injecting the eels with hormones to stimulate their gonads to develop even though they were not migrating through the ocean. Without such injections, eel gonads will not mature in captivity. Such techniques were pioneered in Japan (see the Japanese chapter) and have been effective in producing eggs that have hatched into American eel larvae (Fig. 11.8).

#### Where Have All the Eels Gone?

The American eel is fortunate in having a number of longterm data series to index its abundance and recruitment, particularly in the St Lawrence River and upstream in Lake Ontario. The indices provide information on recruitment and harvest data provide evidence of the size of the exiting spawning stock. An important recruitment index is based on counts at eel ladders on the hydroelectric dams along the St Lawrence. As small eels accumulate below the first dam, densities increase, likely stimulating many eels to move upstream over the fish ladders on the dam, where they are counted daily. Casselman et al. (1997a) and Casselman (2003) reviewed this information and showed that daily ladder passage of upwardly migrating eels at the Moses-Saunders dam on the upper St Lawrence River declined from a peak in 1982/83 to a very low value during the 1990s (Fig. 11.9). The few eels that did ascend were larger and older, but by the late 1990s, the numbers had dropped to virtually zero. Since then, however, a few eels have passed up the ladders, but still far fewer than in the 1980s and earlier (MacGregor et al. 2012; Fig. 11.9). The dramatic decline over the past 20 or so vears is not limited to American eels, however, Catches of glass eels at a long-standing recruitment-monitoring site in the Netherlands have also dropped to virtually zero at times (Dekker 1998), and catches of glass eels of the Japanese species in the North Pacific (Tsukamoto et al. 2009) are now much lower than historically.

These dramatic declines in numbers of eels in North America and elsewhere have served as a wake-up call to scientists monitoring the status of all species of eel. There are indications too that there are fewer American eels in other parts of the species' range (Casselman et al. 1997b; Haro et al. 2000; Casselman 2003), though without such



**Fig. 11.9** Trends in the catches of American eels at the two Moses–Saunders Dam fish ladders, showing the sudden declines in numbers of eels going up and over the dams, and a small increase in numbers in recent years (inset). Modified after MacGregor et al. (2012)

long-term datasets, there is no other equally clear image of a species disappearing from a whole part of a continent. If no eels climb the ladders of the massive dams on the St Lawrence, there will eventually be no eels in the watershed of rivers and lakes upstream of those dams, including in the huge Lake Ontario. Another concern is that the St Lawrence watershed historically supplied large numbers of the big female silver eels migrating back to their spawning area, so with those so scarce now, the total spawning population of the species is likely declining further.

As stated earlier in this chapter, alarm at the continually decreasing recruitment of American, European and Japanese eels stimulated the holding of a special symposium at the 2003 annual meeting of the American Fisheries Society in Québec. That venue was a fitting location for the symposium because at the "narrows" where Québec City now stands, First Nations groups (see below) historically had assembled annually in autumn to negotiate and to catch eels in the St Lawrence River that were present in "an almost unlimited supply" (du Creux 1664), and which "cost nothing beyond the catching" (Thwaites, 1896–1901). That symposium brought together experts on anguillid eels from all around the world, including many of the authors of chapters of this book, to consider what needed to be done to identify and understand the cause of the declines and to evaluate what could be done to protect the various species. The meeting also brought together representatives of the hydropower industry and others working to find ways of helping eels pass over or through dams. It was perhaps one of the most dramatic meetings on eels ever held in North America, with various opinions being expressed on how to approach the problem (see the Panel Discussion in Casselman and Cairns 2009). The synthesized discussions led to the signing of the Québec Declaration of Concern for the status of anguillid eels around the world, which was published soon after the meeting (Dekker et al. 2003), and the story was featured in several articles in journals as prestigious as Nature. The symposium contributions themselves were later published in a book entitled "Eels at the Edge" (Casselman and Cairns 2009; Fig. 11.10). However, there was an unexpected end to the symposium for which the focus had been the struggle of a group of fish species that had existed unchanged for millions of years, that were now simply trying to swim upstream to their ancestral feeding grounds and then to return downstream back to their birthplace. Humankind needs a steady, affordable source of electricity such as from dams, and the day after the symposium ended, the great northeastern electricity blackout struck, cutting the power to millions of people in the northern and eastern US and large regions of Canada. Flights to and from Québec were cancelled and schedules had to be changed. Remarkably, Québec City, the site of the symposium, did not lose power, but it is certain that participants did not fail to see again how society depends

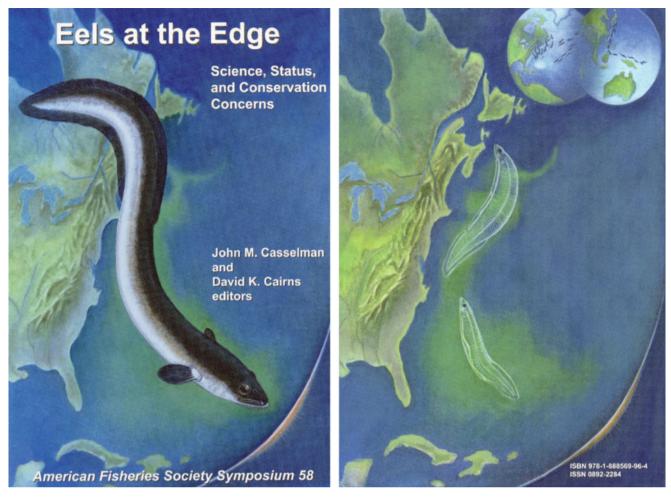


Fig. 11.10 Front and back covers of the Casselman and Cairns (2009) book "Eels at the Edge. Science, Status, and Conservation Concerns" that resulted from the Québec eel symposium in August 2003, when scientists released the "Québec Declaration of Concern" (Dekker et al. 2003)

so much on electricity. However, their resolve to protect and better understand the American eel and other anguillid eels was strengthened by their experience.

One way to address the issue has been to direct research at the factors influencing whether or not eels can safely pass up over or back down through hydroelectric dams (Richkus and Dixon 2003). Various ladder designs had been tried, but eels would pass over some and not others. It was necessary to know, therefore, what combination of location relative to water flow below the dam and what configuration of water flow and gradient inside the ladder would attract the eels and encourage them to move up and over the dam. Similarly, if down-migrating silver eels could be attracted somehow to a particular part of the dam, bypass channels could be provided that would allow them to pass over the dam rather than through the turbines. Scientists and engineers explored a variety of ideas ranging from screens in front of the intakes to producing noise or light to scare the eels away from the intakes. Scientists tagged and tracked eels as they approached the dams to learn about their behaviour and how they reacted to various aspects of the dam or diversions to spillways and passages (Haro and Castro-Santos 2000). However, the eels tended to follow the main water flow into the turbines and were not easily guided by mechanical or behavioural means. Like many species, the huge variation in behaviour of individual eels makes them a difficult creature to control by any method, so the problem of helping them pass over or through dams remains a challenge.

Dams are not the only problem facing the American eel. Loss of habitat has followed the filling-in of wetlands, and overall societal development, pollution and agricultural runoff have reduced the quality of the habitat used by American eels across much of their present range. The decline in recruitment seemed to start after about 1975, corresponding to a major regime shift in the North Atlantic Oscillation (NAO), an atmospheric index related to climate patterns in the region (Hurrell 2005). This led to the hypothesis that some parameter in the ocean might have changed, lowering recruitment, given that immediate spawning success and the survival of larvae likely influence annual recruitment

(Knights 2003; Friedland et al. 2007; Miller et al. 2009). The relationship between the atmosphere and the ocean can affect the productivity of plankton, which could then influence the survival of leptocephali as they are carried in currents across the oceans. American and other eel larvae appear to feed only on particulate organic material referred to as marine snow (Miller et al. 2013), material produced directly from the productivity of the upper ocean, so it is possible that changes in this productivity and the quantity of food available to the larvae could influence the number of eel larvae surviving each year. Correlations have been found between atmospheric factors such as the NAO or sea surface temperature as an indicator of productivity and anguillid eel recruitment (Knights 2003; Bonhommeau et al. 2008). Other factors such as frontal location and ocean currents can also affect the success of larval eel transport from the spawning areas to the coastal habitats where they recruit (Friedland et al. 2007; Miller et al. 2009). This is not the limit of the problems facing eels, however, because introduced parasites can affect their swimbladders, viruses can infect them, and environmental contaminants can weaken them, all of these issues probably compounding to reduce the ability of migrating silver eels to reach their spawning areas successfully.

#### Is the American Eel Endangered?

Relative to other commercially important fish species of North America, the American eel has been largely ignored by national regulatory agencies, for many years. The US National Marine Fisheries Service published a report on the American eel (Fahay 1978) and the US Fish and Wildlife Service (USFWS) and the US Army Corps of Engineers commissioned a report to overview what was known about the species (Facey and Van Den Avyle 1987). However, it was not a priority food or sportfish for Americans, so perhaps US agencies did not pay as much attention to it as they did to high-public-profile species such as striped bass, bluefish, the declining stocks of Atlantic cod, or the endangered Atlantic salmon. That situation changed, however, when two Maine brothers became so distressed at finding silver eels killed by passage through the turbines of dams that they decided to do something about it (Prosek 2010). In the US, any citizen can submit a petition to the USFWS to propose that a species be declared endangered, so this is exactly what the two brothers did. One had worked before on several petitions to list creatures as endangered in Maine, notably the Atlantic salmon, so they were already familiar with procedures, but they still researched the subject carefully and used the data on eel declines in the St Lawrence (see Casselman et al. 1997a; Casselman 2003) to support their case. The USFWS, as was their duty under law, looked into the issue in a 90-day examination in 2005 (USFWS 2005), and they soon realized

that there was insufficient information within their agency or even within any other US government agency to accept or reject the claim of the petition. They therefore initiated a year-long process called a status review, in which experts on all aspects of the species in question were to be assembled for a series of workshop-type meetings to present the existing state of knowledge about the species. For the American eel, this meant that scientific experts on the life of these eels in both freshwater and the ocean needed to be included, as well as experts on the technicalities of barriers. The goal of the process was to collect sufficient information to make an informed decision about whether or not the American eel was endangered. Although it was a serious occasion, at the end of one workshop session the question was posed whether anyone had anything else to add, especially something giving a perspective from a different side. Some additional information was then shared before one scientist who studied American eels produced a poem:

More eels Eels in the ocean Eels in the stream Eels in the turbines, I could just scream!

More eels for sushi More eels for bass This eel decline Is quite a morass!

We all want more eels Don't know who's the worst But more eels for elvers Have got to come first!

# *Paul Angermeier (from the American eel USFWS Workshop Minutes).*

After the public process of gathering information from the experts, the USFWS evaluated the information and concluded that the American eel was neither threatened nor endangered (USFWS 2007). Their conclusion was presented in a short summary: "We, the US Fish and Wildlife Service (USFWS), announce our 12-month finding on a petition to list, under the Endangered Species Act of 1973 (Act), as amended, the American eel (A. rostrata) as a threatened or endangered species throughout its range. After a thorough review of all available scientific and commercial information, we find that listing the American eel as either threatened or endangered is not warranted at this time. We ask the public to continue to submit to us any new information that becomes available concerning the status of or threats to the species. This information will help us to monitor and encourage the ongoing conservation of this species." That statement was followed by a 31-page report on the scientific and technical details of the findings (USFWS 2007). This outcome, or at least the way the report approached the issue, was a surprise to those who had petitioned the USFWS (Prosek 2010), but with eel recruitment continuing each year with no evidence of massive disappearance of eels except in the St Lawrence River drainage, there was no scientific basis upon which to conclude otherwise. Despite that finding, another petition has been filed to the USFWS recently (CESAR 2010).

In Canada, however, a wider range of actions was already underway. In 2004, the Ontario Ministry of Natural Resources officially closed all commercial fishing for eels as a result of the dramatic decline of eels in the St Lawrence River system, the first and only jurisdiction in the world to have taken such an action for anguillid eels. In 2007, eels in Ontario were officially classified as endangered under the Ontario Endangered Species Act (MacGregor et al. 2012). The Canadian government listed the status of the American eel as being of special concern in 2006 and as being threatened in May 2012 (COSEWIC 2012), resulting in a Recovery Strategy being put into place with recommendations and approaches to increase the escapement of silver eels and recruitment (MacGregor et al. 2012). Further, in the US also in May 2012, the Atlantic States Marine Fisheries Commission (ASMFC) circulated a press release indicating that their benchmark assessment recently completed had confirmed that the American eel stock in US waters was depleted (ASMFC 2012).

In Canada too, because of their long, well-documented association with eels, Donald Marshall and the Mi'kmaq First Nations people used their experience with eels and eel fishing to argue, in the Supreme Court of Canada, that they had a treaty right to harvest marine resources for commercial purposes. They won that landmark decision (Supreme Court of Canada, R. V. Marshall 1999(3): 3ff). Then in 2008, Aboriginals assembled in Ottawa, Canada, to discuss the status of the eel and prepared an official Aboriginal People's American Eel Resolution. It called for a number of actions, including that the export fishery for glass eels be closed (i.e. glass eels were only to be used for conservation stocking) and that the American eel in Canada be considered as threatened. The indication was therefore that Aboriginals would give up many of their longstanding rights to using eels to see them restored. This resolution was signed by Aboriginal elders from across the range of eels in Canada, from the Algonquins of Ontario to the Mi'kmaq of the Maritimes (including Donald Marshall). Aboriginal concerns about the declining American eel and their long, welldocumented association with the fish, which they considered to be an important reflection of their identity, led to a thoughtprovoking document by the Algonquins of Ontario expressing the desire to see eels returned to the large Ottawa River Basin (Algonquins of Ontario 2012), where they are now virtually absent because of the extensive construction of numerous large dams many years ago (MacGregor et al. 2012).

Much has been done since the 2003 Québec Declaration of Concern to restore the world's anguillid eels, but compared with the European eel that has been Red Listed by the International Union for Conservation of Nature (IUCN), the American eel is managed less intensively. The European eel was proposed for listing in Appendix II of CITES, and listing came into force in March 2009. In December 2010, European Union member states suspended all exports and imports of European eel commodities, probably placing further pressure on the American eel because the extensive worldwide culture of eels was left to depend almost entirely upon American glass eels and elvers, likely affecting the recovery plans for the species.

It is obvious that concerns about the status of the American eel are now considerable, and international cooperation and coordination is needed to help protect a species that has massively reduced watersheds in which to live before returning to the ocean to spawn. Therefore, the size of its population must be much smaller than it was historically. Awareness of this is a first step in learning how one may help the species survive in the ever-changing world. Understanding eels from all perspectives of our relationships with them is important in facilitating efforts to protect them and educating the general public about them. A recent book, "Eels on the Move: mysterious creatures over millions of years" by the current guest editors (Kuroki and Tsukamoto 2012) overviewed a range of subjects including the biology, life history and cultural aspects of how humanity has viewed eels and used them for food. It offers a unique view into what scientists have learned about eels and the relationship between human society and eels. As awareness of eels increases worldwide through similar books and the present one, and efforts to conserve eels intensify, the American eel will hopefully provide refreshed hope that humankind and eels can live together and flourish as they share the waters of the rivers, lakes and estuaries of eastern North America for millennia to come.

Acknowledgements Knowledge of the relationships between the American eel and humankind by many others gave the perspective needed for us to write parts of this chapter. In addition, Alex J. Haro provided some of the artwork material, and James Prosek willingly gave both useful information and artwork material.

#### References

- Algonquins of Ontario (2012) Returning Kichisippi Pimisi—the American eel—to the Ottawa River basin. Algonquins of Ontario consultation office, Pembroke, 14 pp
- ASMFC (Atlantic States Marine Fisheries Commission) (2012) ASMFC stock assessment overview: American eel, May 2012, 6 pp. www.asmfc.org
- Boëtius J, Harding EF (1985) A re-examination of Johannes Schmidt's Atlantic eel investigations. Dana 4:129–162
- Bonhommeau S, Chassot E, Planque B, Rivot E, Knap AH, Le Pape O (2008) Impact of climate on eel populations of the northern hemisphere. Mar Ecol Progress Ser 373:71–80
- Casselman JM (2003) Dynamics of resources of the American eel, Anguilla rostrata: declining abundance in the 1990s. In: Aida K,

Tsukamoto K, Yamauchi K (eds) Eel biology. Springer, Tokyo, pp 255–274

Casselman JM, Cairns DK (eds) (2009) Eels at the edge: science, status, and conservation concerns. Proceedings of the 2003 international eel symposium, vol 58. American Fisheries Society Symposium, Bethesda, MA

Casselman JM, Marcogliese LA, Hodson PV (1997a) Recruitment index for the upper St. Lawrence River and Lake Ontario eel stock: a re-examination of eel passage at the R. H. Saunders hydroelectric generating station at Cornwall, Ontario, 1974–1995. In: Peterson RH (ed) The American eel in eastern Canada: stock status and management strategies. Proceedings of the eel workshop, Québec City, 13–14 January 1997, Can Tech Rep Fish Aquat Sci 2196:161–169

- Casselman JM, Marcogliese LA, Stewart T, Hodson PV (1997b) Status of the upper St. Lawrence River and Lake Ontario American eel stock—1996. In: Peterson RH (ed) The American eel in eastern Canada: stock status and management strategies. Proceedings of the eel workshop, Québec City, 13–14 January 1997, Can Tech Rep Fish Aquat Sci 2196:106–120
- Castonguay M, Hodson PV, Couillard CM, Eckersley MJ, Dutil JD, Verreault G (1994) Why is recruitment of the American eel, *Anguilla rostrata*, declining in the St Lawrence River and Gulf? Can J Fish Aquat Sci 51:479–488
- CESAR (Council for Endangered Species Act Reliability) (2010) Petition to list American eel (*Anguilla rostrata*) as a threatened species under the endangered species act. www.fws.gov/northeast/ newsroom/pdf/American\_eel\_petition\_100430.pdf
- Chow S, Kurogi H, Mochioka N, Kaji S, Okazaki M, Tsukamoto K (2009) Discovery of mature freshwater eels in the open ocean. Fish Sci 75:257–259
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2012) COSEWIC assessment and status report on the American eel *Anguilla rostrata* in Canada. Committee on the status of endangered wildlife in Canada, Ottawa. xii+, 109 pp. www. registrelep-sararegistry.gc.ca/default\_e.cfm
- Dekker W (1998) Long-term trends in the glass eels immigrating at Den Oever, the Netherlands. Bull Fr Peche Piscic 349:199–214
- Dekker W, Casselman JM, Cairns DK, Tsukamoto K, Jellyman D, Lickers H (2003) Worldwide decline of eel resources necessitates immediate action: Québec declaration of concern. Fisheries 28:2830
- du Creux E (1664) History of Canada or New France, vol 1. The Champlain Society, Toronto
- Facey DE, Van Den Avyle MJ (1987) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): American eel. Biological report 82(11.74). Biological report US fish and wildlife service 82(11.74). US Army Corps of Engineers, TR EL-82-4, 1987, 28 pp
- Fahay MP (1978) Biological and fisheries data on American eel, *Anguilla rostrata* (LeSueur). US Department of Commerce, national marine service technical report, vol 17, Northeast Fisheries Center, Highlands, 82 pp
- Friedland KD, Miller MJ, Knights B (2007) Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel. ICES J Mar Sci 64:519–530
- Haro A (2003) Downstream migration of silver phase anguillid eels. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel biology. Springer, Tokyo, pp 215–222
- Haro AJ, Castro-Santos T (2000) Behavior and passage of silver phase American eels, *Anguilla rostrata* (LeSueur), at a small hydroelectric facility. Dana 12:33–42
- Haro AJ, Krueger WH (1988) Pigmentation, size, and migration of elvers (*Anguilla rostrata* (Lesueur)) in a coastal Rhode-Island stream. Can J Zool 66:2528–2533
- Haro A, Richkus W, Whalen K, Hoar A, Busch W-D, Lary S, Brush T et al (2000) Population decline of the American eel: implications for research and management. Fisheries 25:7–16

- Helfman GS, Clark JB (1986) Rotational feeding: overcoming gapelimited foraging in anguillid eels. Copeia 1986:679–685
- Helfman GS, Facey DE, Hales S, Bozeman EL (1987) Reproductive ecology of the American eel. In: Dadswell MJ, Klauda RJ, Moffitt CM, Saunders RL, Rulifson RA, Cooper JE (eds) Common strategies of anadromous and catadromous fishes, vol 1. American Fisheries Society Symposium, Bethesda, pp 42–56
- Hjort J (1910) Eel larvae from the central Atlantic. Nature 85:104–106
- Hurrell JW (2005) Decadal trends in the North Atlantic oscillation: regional temperatures and precipitations. Science 269:676–679
- Jessop BM (2010) Geographic effects on American eel (Anguilla rostrata) life history characteristics and strategies. Can J Fish Aquat Sci 67:326–346
- Jessop BM, Cairns DK, Thibault I, Tzeng WN (2008) Life history of American eel Anguilla rostrata: new insights from otolith microchemistry. Aquat Biol 1:205–216
- Junker-Andersen C (1988) The eel fisheries of the St Lawrence Iroquoians. North Am Archaeol 9:97–121
- Kleckner RC, McCleave JD (1985) Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current systems. Dana 4:67–92
- Kleckner RC, McCleave JD (1988) The northern limit of spawning by Atlantic eels (*Anguilla* spp.) in the Sargasso Sea in relation to thermal fronts and surface water masses. J Mar Res 46:647–667
- Kleckner RC, McCleave JD, Wippelhauser GS (1983) Spawning of American eel, Anguilla rostrata, relative to thermal fronts in the Sargasso Sea. Environ Biol Fish 9:289–293
- Knights B (2003) A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the northern hemisphere. Sci Total Environ 310:237–244
- Krueger WH, Oliveira K (1999) Evidence for environmental sex determination in the American eel. Environ Biol Fish 55:381–389
- Kuroki M, Tsukamoto K (2012) Eels on the move: mysterious creatures over millions of years. Tokai University Press, Tokyo, 278 pp
- MacGregor R, Casselman J, Greig L, Dettmers J, Allen WA, McDermott L, Haxton T (2012) Draft recovery strategy for the American eel (*Anguilla rostrata*) in Ontario. Ontario recovery strategy series. Prepared for Ontario Ministry of Natural Resources, Peterborough, Ontario, x +pp 128+ Appendices
- McCleave JD (2001) Simulation of the impact of dams and fishing weirs on reproductive potential of silver-phase American eels in the Kennebec River Basin, Maine. North Am J Fish Manag 21: 592–605
- McCleave JD (2003) Spawning areas of the Atlantic eels. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel biology. Springer, Japan, pp 141–155
- McCleave JD, Kleckner RC (1982) Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). J Cons Int Explor Mer 40:262–271
- McCleave JD, Kleckner RC, Castonguay M (1987) Reproductive sympatry of American and European eels and implications for migration and taxonomy. In: Dadswell MJ, Klauda RJ, Moffitt CM, Saunders RL, Rulifson RA, Cooper JE (eds) Common strategies of anadromous and catadromous fishes, vol 1. American Fisheries Society Symposium, Bethesda, pp 286–297
- Miller MJ, McCleave JD (1994) Species assemblages of leptocephali in the subtropical convergence zone of the Sargasso Sea. J Mar Res 52:743–772
- Miller MJ, Kimura S, Friedland KD, Knights B, Kim H, Jellyman DJ, Tsukamoto K (2009) Review of ocean-atmospheric factors in the Atlantic and Pacific oceans influencing spawning and recruitment of anguillid eels. In: Haro AJ, Smith KL, Rulifson RA, Moffitt CM, Klauda RJ, Dadswell MJ, Cunjak RA et al (eds) Challenges for diadromous fishes in a dynamic global environment, vol 69. American Fisheries Society Symposium, Bethesda, pp 231–249

- Miller MJ, Chikaraishi Y, Ogawa NO, Yamada Y, Tsukamoto K, Ohkouchi N (2013) A low trophic position of Japanese eel larvae indicates feeding on marine snow. Biol Lett 9:20120826
- Munk P, Hansen MM, Maes GE, Nielsen TG, Castonguay M, Riemann L, Sparholt H et al (2010) Oceanic fronts in the Sargasso Sea control the early life and drift of Atlantic eels. Proc R Soc Ser B 277: 3593–3599
- Oliveira K (1999) Life history characteristics and strategies of the American eel, *Anguilla rostrata*. Can J Fish Aquat Sci 56:795–802
- Oliveira K, Hable WE (2010) Artificial maturation, fertilization, and early development of the American eel (*Anguilla rostrata*). Can J Zool 88:1121–1128
- Oliveira K, McCleave JD (2000) Variation in population and life history traits of the American eel, *Anguilla rostrata*, in four rivers in Maine. Environ Biol Fish 59:141–151
- Orr RB (1917) Ontario Indians: their fish, fisheries, and fishing appliances. 29th annual archaeological report. King's Printer, Toronto, pp 24–43
- Parker SJ (1995) Homing ability and home range of yellow-phase American eels in a tidally dominated estuary. J Mar Biol Assoc UK 75:127–140
- Pennisi E (1991) Gone eeling: luck and science face off in two eelseeking adventures. Sci News 140:297–299
- Prosek J (2010) Eels: an exploration, from New Zealand to the Sargasso, of the world's most mysterious fish. Harper–Collins, New York, p 287
- Richkus WA, Dixon DA (2003) Review of research and technologies on passage and protection of downstream migrating catadromous eels at hydroelectric facilities. In: Dixon DA (ed) Biology, management, and protection of catadromous eels, vol 33. American Fisheries Society Symposium, Bethesda, pp 377–388
- Schmidt J (1922) The breeding places of the eel. Phil Trans R Soc B 211:179–208
- Schmidt J (1927) Eel larvae in the Faroe channel. J Cons Int Explor Mer 2:38–43
- Schmidt J (1935) Danish eel investigations during 25 years (1905–1930). The Carlsberg Foundation, Copenhagen, 16 pp
- Schoth M, Tesch F-W (1982) Spatial distribution of 0-group eel larvae (Anguilla sp.) in the Sargasso Sea. Helgoländer Meeresun 35: 309–320
- Shinoda A, Aoyama J, Miller MJ, Otake T, Mochioka N, Watanabe S, Minegishi Y et al (2011) Evaluation of the larval distribution and

migration of the Japanese eel in the western North Pacific. Rev Fish Biol Fish 21:591-611

- Tesch F-W (2003) The eel: biology and management of anguillid eels. Blackwell, London
- Tesch F-W, Wegner G (1990) The distribution of small larvae of *Anguilla* sp. related to hydrographic conditions 1981 between Bermuda and Puerto Rico. Int Rev Hydrobol Hydrogr 75: 845–858
- Thwaites RG (1903) A new discovery of a vast country in America, by Father Louis Hennepin. A. C. McClurg and Co, Chicago
- Tsukamoto K (1992) Discovery of the spawning area for Japanese eel. Nature 356:789–791
- Tsukamoto K, Aoyama J, Miller MJ (2009) The present status of the Japanese eel: resources and recent research. In: Casselman JM, Cairns DK (eds) Eels at the edge: science, status, and conservation concerns, vol 58. American Fisheries Society Symposium, Bethesda, pp 21–35
- Tsukamoto K, Chow S, Otake T, Kurogi H, Mochioka N, Miller MJ, Aoyama J et al (2011) Oceanic spawning ecology of freshwater eels in the western North Pacific. Nat Commun 2:179
- Tsukamoto K, Mochioka N, Miller MJ, Koyama S, Watanabe S, Aoyama J (2013) Video observation of an eel in the *Anguilla japonica* spawning area along the West Mariana Ridge. Fish Sci 79:407–416
- USFWS (United States Fish and Wildlife Service) (2005) Endangered and threatened wildlife and plants; 90-day finding on a petition to list the American eel as threatened or endangered. Fed Reg 70(128):38849–38861
- USFWS (United States Fish and Wildlife Service) (2007) Endangered and threatened wildlife and plants; 12-month finding on a petition to list the American eel as threatened or endangered. Fed Reg 72(22):4967–4997, Available at www.archives.gov
- Verreault G, Pettigrew P, Tardif R, Pouliot G (2003) The exploitation of the migrating silver American eel in the St. Lawrence River estuary, Québec, Canada. In: Dixon DA (ed) Biology, management, and protection of catadromous eels, vol 33. American Fisheries Society Symposium, Bethesda, pp 225–234
- Wippelhauser GS, McCleave JD (1988) Rhythmic activity of migrating juvenile American eels (Anguilla rostrata LeSueur). J Mar Biol Assoc UK 68:81–91
- Wirth T, Bernatchez L (2003) Decline of North Atlantic eels: a fatal synergy? Proc R Soc London B 270:681–688