in many habitats—not only disturbed ones—finally led to the recognition that invasions were an integral and global problem, not just a collection of intriguing and sometimes troubling special cases. This was the raison d'être of the SCOPE program, and it is unsurprising that other scientists would have recognized the same phenomenon at roughly the same time.

A second reason the SCOPE program was timely is that the 1980s were a time of intense interest in various academic theories (especially in population and community biology) and their potential relevance to ecological problems; among these were the dynamic equilibrium theory of island biogeography, theories of limiting similarity, and theoretical explorations of the relationship between stability of biotic communities and their diversity or complexity. Data on introduced species seemed appropriate to test such ideas, and several contributions to the SCOPE volumes used them to just that end. Quantitative treatment and modeling were prominent features of many parts of the SCOPE program and have remained a key component of modern invasion biology. Elton's monograph, by contrast, was largely a collection of particular cases and interesting anecdotes.

The SCOPE project, then, was the proximate impetus behind the explosive growth of modern invasion biology beginning in the 1980s. It did not address all aspects of the current invasion biology agenda. For instance, evolutionary questions had a low profile in the SCOPE project (and virtually no profile in Elton's monograph), and evolution of both invaders and members of invaded communities became an important part of the field by the late 1990s. However, the three SCOPE questions—what makes some species invasive, what makes some systems invasible, and how information on these matters can inform management—remain major components of invasion biology.

SEE ALSO THE FOLLOWING ARTICLES

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SEA LAMPREY

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The sea lamprey (*Petromyzon marinus*) is an ancient and parasitic fish that invaded the Laurentian Great Lakes from its native habitat in the coastal regions of the North Atlantic. Its complex anadromous life cycle includes both a filter-feeding larval phase, during which it lives burrowed in freshwater stream sediments, and a parasitic phase, during which it lives in saltwater, where it feeds voraciously on the blood of other fish before returning to freshwater streams to reproduce. The sea lamprey invaded the Laurentian Great Lakes in the early twentieth century, adopted a freshwater lifestyle, and within a few decades had triggered a near total collapse of this ecosystem's fisheries. Since the 1950s, it has been the focus of one of the world's only successful invasive fish control program, resulting in a substantial, albeit partial, recovery of Great Lakes fisheries. This control program relies mainly on taxon-specific toxicants and barriers but is developing new approaches, including the release of sterile males and pheromone-mediated trapping. Ironically, the sea lamprey is now threatened across much of its original range, where it is considered a delicacy.

From Daniel Simberloff and Marcel Rejmánek, editors, *Encyclopedia of Biological Invasions*, Berkeley and Los Angeles: University of California Press, 2011.

THE SPECIES, ITS BIOLOGY AND LIFE HISTORY

The sea lamprey, *Petromyzon marinus*, is an ancient, jawless cartilaginous fish that has changed little over the past 400 million years (Fig. 1). It is native to coastal regions of both the European and North American sides of the Atlantic Ocean and is closely related to three dozen other species of northern hemisphere lampreys, none of which are invasive. The sea lamprey has a complex anadromous life history that includes a filter-feeding larval stage, during which it usually lives burrowed in sediments of freshwater streams; a juvenile parasitic stage, during which it usually lives in saltwater, where it feeds on the blood of host fishes; and an adult stage,

FIGURE 1 Drawing of a sexually mature adult sea lamprey. Image originally prepared by Ellen Edmonson and Hugh Chrisp as part of the 1927–1940 New York Biological Survey. (Permission for use granted by the New York State Department of Environmental Conservation [NYSDEC].)

when it enters freshwater streams to spawn and die (Fig. 2). In the past century, the sea lamprey has invaded a number of North American lakes including the Laurentian Great Lakes (see section below), where it appears to continue to pursue the same life history strategies with just a few minor exceptions. The sea lamprey is by far the best understood of the lampreys, especially in the Great Lakes, where it is invasive and its presence has promoted intensive study.

The life history of the sea lamprey is complex and is key to both its success and control. Adult sea lampreys migrate into freshwater streams from their oceanic or lacustrine feeding habitat in May and June each year. Mature males, which have a distinctive rope-like dorsal ridge, use their oral discs like a suction cup to move stones into horseshoe-shaped nests (*Petromyzon* means "stone sucker" in Latin). Sea lampreys are fecund: Atlantic Ocean females carry between 150,000 and 300,000 eggs, while Great Lakes fish have 20,000 to 110,000 eggs. Ripe males attract females to their nests by releasing a steroidal sex pheromone. After depositing fertilized eggs into nests, males and females die. Eggs hatch within about a week into tiny, blind, filter-feeding larvae, known as ammocoetes. Larvae burrow in stream sediments and filter-feed on biofilm sloughed from the substrate. The ecological significance of this activity is considerable, as some Great Lakes streams have hundreds of thousands of larval lampreys of multiple species. Once larval sea lampreys reach a length of about 120 mm (in the Great Lakes, this takes between 3 and 20 years), they undergo a radical metamorphosis and develop eyes, a greatly enlarged olfactory system, and an oral disc that they later use to attach to host fish (Fig. 3). Metamorphosed sea lampreys leave streams between late fall and spring to enter the Atlantic Ocean or freshwater lakes.

Juvenile sea lampreys are voracious predators and use their well-developed oral discs with proteinacious teeth to attach to host fishes and bore a hole so they can then suck blood and body fluids. Estimates of the biomass and number of fish killed per sea lamprey vary widely but range up to 20 kg per lamprey. Parasite growth rates are greatest in late autumn, and recoveries of dead fish in the Great Lakes suggest that this is when most fish are killed. When lake trout are abundant, they bear a disproportionate number of sea lamprey attacks, but all large fish are vulnerable to attack, and apparent host preferences may simply be due to parasite and host depth and temperature distributions. When feeding, sea lampreys are typically carried far from their natal streams by their hosts and become widely dispersed.

The parasitic stage of sea lampreys is thought to last two seasons in the Atlantic Ocean but is known (through tagging) to last only one in the Great Lakes. Adult lampreys reach an average length of 50 cm in the

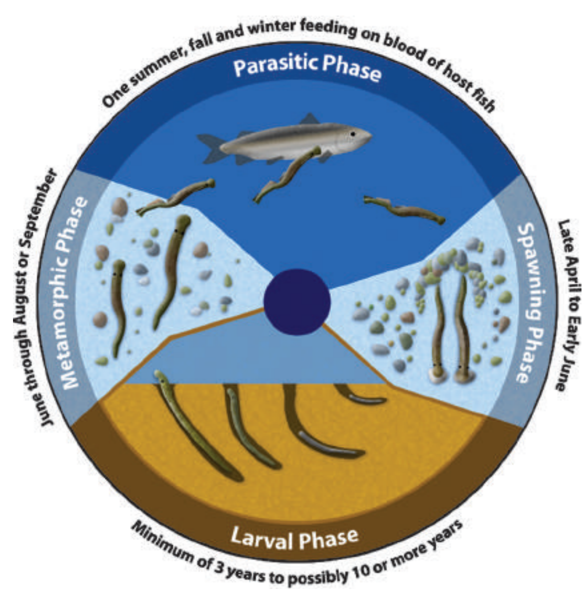

FIGURE 2 Life history of the sea lamprey. (Courtesy of the Great Lakes Fishery Commission.)

FIGURE 3 Oral disc of a parasitic-phase sea lamprey. The animal uses this sucker-like structure to attach to its prey and then cuts a hole into the prey using the sharp cusps on its "tongue." (Photograph courtesy of Ted Lawrence, Great Lakes Fishery Commission.)

Great Lakes by late winter, when they start to mature and search for spawning streams that they enter in early spring. Field studies have demonstrated that sea lampreys do not return to natal streams, but instead choose (locate) streams that contain large numbers of larvae. This feat appears attributable to a larval pheromone that is composed of unique sulfated sterols. It is the only migratory pheromone identified and synthesized in a fish and is active at concentrations below 10^{-13} Molar (a gram in 80 billion liters). Reliance on a pheromone makes evolutionary sense for a species that may be transported far from its natal stream by its host and for which the larvae odor can serve as a universal indicator of spawning and nursery habitat.

The sea lamprey has a remarkable physiology. It is an extremely robust animal and undergoes two radical metamorphoses (first to a parasitic and then to an adult phase) and has a sophisticated kidney that functions in either full strength sea water or the low-ion waters of the Great Lakes. While the sea lamprey's eyesight is relatively poor and its taste system primitive, it has one of the most developed and specialized olfactory systems of the vertebrates (its nose is about a third the size of its brain)—a trait that allows it to use pheromones to great advantage in its expansive environment. Like most ancient fishes, it also is sensitive to electric fields and possesses some unusual enzyme systems, which make it susceptible to certain toxicants (see below). It is a surprisingly persistent swimmer, has an indeterminate growth rate, and is fecund—all traits that give it enormous flexibility and contribute to its invasiveness.

INVASIVE PATHWAYS AND DAMAGE

The sea lamprey has been a valued fish since the Middle Ages in Europe, where it served as food for both commoners and royalty and seems to have caused no problems (although King Henry I of England died of eating a "surfeit of lamprey pie"). Apparently, the sea lamprey was not eaten by indigenous peoples in North America, although its close relative, the Pacific lamprey (*Entosphenus tridentate*), was (and still is). By all indications, sea lampreys played a balanced role in coastal food webs prior to settlement. This situation changed quickly at the end of the nineteenth century in North America, with the construction of shipping canals that allowed ships to enter the Great Lakes and other inland lake systems. With the exception of Lake Ontario, these lakes had been isolated since their formation at the end of the last glaciations by Niagara Falls and had evolved simple but productive ecosystems that also came to support huge inland fisheries. Within a few decades of the construction and enlargement of these canals (especially the Welland Canal that bypasses Niagara Falls), the sea lamprey was observed in Lake Erie (Fig. 4). Sea lampreys were subsequently observed in rapid succession in lakes Huron, Michigan, and Superior during the course of the 1930s, at which time self-sustaining populations developed and flourished. The sea lamprey also became prevalent (and problematic) in the Finger Lakes of New York and in Lake Champlain. Although the details of how and when it spread and whether it may have originally been native in some of these systems are unclear, the dramatic increase in its numbers is not.

At the same time that sea lamprey numbers increased in the Great Lakes, fish populations collapsed dramatically. In particular, the lake trout (*Salvelinus namaycush*),

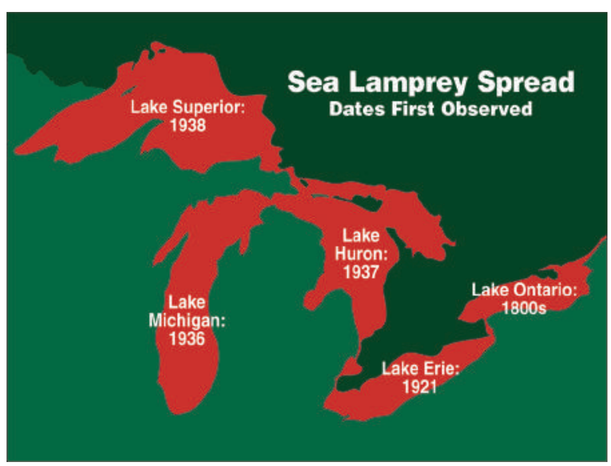

FIGURE 4 Dates of the first documented observation of sea lampreys in each of the Great Lakes. (Courtesy of the Great Lakes Fishery Commission.)

a keystone predator in the Great Lakes, was the first to suffer severe losses, and by the late 1940s, fisheries for them had collapsed with devastating economic and ecological consequences. Although some argue that initial decreases may have been promoted by overfishing and pollution, the strikingly inverse relationship between lamprey and lake trout abundance suggests an important link. Lake trout became extinct in all of the Great Lakes except Superior by the end of the 1950s. This change caused dramatic, cascading changes in the fish communities and lake ecology. With the reduction in predators came explosions in the populations of invasive "prey" species such as smelt and alewives, followed by massive annual die-offs of many during the 1950s and 1960s (Fig. 5). These events caused tremendous, but never estimated, losses in property and recreational value. Extinctions of deepwater sculpins in Lake Ontario and several deepwater coregonine fishes across the Great Lakes also coincided with extended periods of high abundance of prey fishes. After initial success controlling the sea lamprey, government agencies attempted to stabilize these systems by stocking large numbers of native lake trout along with nonnative species of trout and Pacific salmon. Those additions (which continue at a reduced level) have resulted in viable recreational fisheries and stabilized fish communities. The Great Lakes ecosystem continues to change and remains in a state of flux (see below), as other invaders continue to enter this system and agencies continue their efforts to control them. Similar versions of this scenario play out in the Finger Lakes and Lake Champlain.

FIGURE 5 Photograph of a mass die-off of alewives in the Great Lakes, which can be attributed to predator–prey imbalances associated with the invasion of the sea lamprey. (Photograph courtesy of the Great Lakes Fishery Commission.)

Ironically, at the same time that the number of sea lampreys exploded in the Great Lakes, the abundance of this fish plunged across most of the Atlantic coast, especially in Europe. Most believe that dams, declining water quality, and overfishing (the sea lampreys are prized as food by the Portuguese and Finns) have been and continue to be responsible. Several reasons seem to explain why sea lamprey should be invasive in the large inland lakes of North America. Here, key waterways were opened up to shipping and not blocked by dams. Perhaps most importantly, their simple ecosystems seem both to lack predators for sea lampreys and to contain large spawning and nursery habitats previously occupied by native lampreys. Sea lampreys could quickly locate that habitat by following pheromone trails left by once abundant (and beneficial) native lampreys that also appear to excrete the same migratory pheromone. Lastly, larger fishes native to the Great Lakes had evolved no defense mechanisms for predators.

SEA LAMPREY CONTROL

Control of the sea lamprey in the Great Lakes is one of only a few success stories for an invasive fish. Efforts started in the late 1940s, when the State of Michigan began studying the biology of the sea lamprey to identify key aspects of its unusual life cycle that could be exploited. In 1950 the U.S. Fish and Wildlife Service assumed these efforts. In 1955, after a continuing deterioration in lake fisheries, the binational Great Lakes Fishery Commission (GLFC) was formed under a convention between the United States and Canada. One of the GLFC's primary duties was (and is) the control or eradication of sea lampreys, and it currently funds and oversees management of sea lamprey populations across the Great Lakes. Control is delivered through U.S. and Canadian government agents.

Control of the sea lamprey has focused on breaking its life cycle at vulnerable points: adult migration and larval survival. Early control efforts used screen weirs, often in conjunction with electrical fields, to block access to the spawning areas and trap and remove adult spawners. However, this proved only partially effective, and a screening program to find a selective toxicant was initiated in the early 1950s. It evaluated over 6,000 chemicals before identifying 3-trifluoromethyl-4-nitrophenol (TFM), which interferes with oxidative phosphorylation. Selectivity is attributable to the lamprey's lack of an enzyme to break down TFM. Starting in Lake Superior in 1958, TFM has been carefully applied as a "lampricide" to infested streams. A second, nonselective toxin, 2′, 5-dichloro-4′-nitrosalicylanilide (niclosamide) is also occasionally used in conjunction with TFM in high-alkalinity waters to enhance potency and selectivity. Only streams heavily infested with sea lamprey larvae are currently treated with lampricides, and then only when the larvae are large enough to metamorphose. These streams are identified by yearly surveys. Fortunately, of over 5,000 tributaries to the Great Lakes, only 474 have historically produced sea lampreys, and only 284 regularly require treatments. Notably, extensive toxicity studies permit the concentration of TFM to be precisely gauged relative to flow, temperature, pH, and water chemistry. Treatments rarely kill significant numbers of nontarget organisms, with the exception of native lampreys and some insects. Although niclosamide and TFM degrade rapidly with sunlight and wave action, do not bioaccumulate, and have no known effects on higher vertebrates, their use can promote controversy. Lampricide treatments have proven highly successful, leading to a decrease in sea lamprey numbers to about 10 percent of their former numbers. Reduced lamprey numbers have allowed native and stocked fish to survive and the lake trout populations to rebound. Recently, the restoration of lake trout in Lake Superior was declared a success, and most stocking stopped. A substantial, although much changed, fishery once again exists in the Great Lakes, as well as in Lake Champlain and the Finger Lakes.

New control strategies are being developed to enhance an integrated control program that relies less on expensive toxicants. Ineffective screen weirs have been replaced with low-head barriers that block sea lampreys but allow jumping fish to pass. Adjustable-height barriers and electrical barriers that use safe levels of pulsed DC current are also in use. A new technique is the release of male sea lampreys sterilized by injection with a biodegradable mutagenic chemical (bisazir) administered in a self-contained facility that eliminates environmental release. Bisazir makes sperm nonviable without affecting behavior. Sterile males are released into the last large untreated population in the Great Lakes, the St. Marys River, where it is hoped they can nullify the success of other males. Some success is indicated. Lastly, sex and migratory pheromones of the sea lamprey have now been identified and synthesized. The migratory pheromone is being explored as a potent and safe attractant to bring migratory sea lampreys into spawning systems while the sex pheromone is being examined for its ability to trap females on spawning grounds. Most recently, the sea lamprey genome has been mapped, and research is also under way to understand better which genes regulate key processes in the development and sexual maturation of sea lampreys. Many interesting challenges await those seeking to understand and manage this enigmatic, extremely damaging invasive animal.

SEE ALSO THE FOLLOWING ARTICLES

Biological Control, of Animals / Canals / Fishes / Great Lakes: Invasions / Lakes / Life History Strategies / Parasites, of Animals / Pesticides (Fish and Mollusc)

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SEAS AND OCEANS

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The patterns of invasion in the ocean realm are obvious in that they clearly reflect the human footprint of global commerce and overexploitation of natural resources. However, there are significant exceptions to the expected patterns, with some regions seemingly much less invaded than others despite being subject to generally similar frequencies of ship traffic, urbanization of the coastal region, and other characteristics that are broadly associated with increased levels of invasion. Also, certain taxa, despite significant commercial interest and opportunities for intentional introductions, unlike similar taxa in terrestrial habitats, have not been the focus of introduction.

TAXONOMIC LIMITS OF INVASIONS

The extent of invasions in marine seas and oceans involves a broad array of taxa, including fishes, invertebrates, and algae. Many entries in this volume address the diversity of the many groups that are introduced species. However,