The Environmental Consequences of Alien Species in the Swedish Lakes Mälaren, Hjälmaren, Vänern and Vättern

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Source: AMBIO: A Journal of the Human Environment, 30(8) : 514-521

Published By: Royal Swedish Academy of Sciences

URL: https://doi.org/10.1579/0044-7447-30.8.514

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The Environmental Consequences of Alien Species in the Swedish Lakes Mälaren, Hjälmaren, Vänern and Vättern

Twenty alien species have become established in the lakes Mälaren, Vänern, Vättern and Hjälmaren. Intentional introductions include fish and the signal crayfish from North America, ornamental plants, and the Canada goose. Unintentional introductions include the crayfish plague introduced with infected crayfish, the zebra mussel, and Chinese mitten crab introduced with ballast water. The introduction of pathogens and parasites, in particular the crayfish plague, to the lakes has had the greatest environmental and socioeconomic effects and has contributed to the decimation of the indigenous noble crayfish. The stocking of brown trout and salmon with origins from different biogeographical regions has contributed to the extinction of relict indigenous fish species in L. Vänern. Although major ecosystem damage caused by the introduction of alien species, with the exception of the crayfish plague, has not occurred in the four large Swedish lakes, local problems of considerable dignity occur occasionally.

INTRODUCTION

Throughout history, in their attempts to improve their quality of life, humans have continuously introduced alien plants and animals to new areas. The introduction of alien species (Box 1) to new environments, as well as the destruction of habitats and the exploitation of land and water are all major threats to the biological diversity of freshwaters (1). With the introduction of alien species habitats may be altered, structures and functions of ecosystems may be disrupted, and indigenous species and their genetic adaptations are often affected or altered due to increased competition, predation or hybridization (2, 3). The genetic consequences of the introduction of alien species or populations can be hybridization between different species or populations and the loss of local genetic adaptations with genetic depletion as a result.

Internationally introduced species have unquestionably been responsible for major changes in aquatic ecosystems including extinction of native species. One example is the introduction of 14 alien fish species to the Aral Sea in the former Soviet Union to improve fisheries, which resulted in reducing populations of endemic fish by half, through the introduction of a gill parasite and competition for food with a subsequent depletion of zooplankton biomass (3). Another example is the intentional and unintentional introduction of more than 145 species of fish, invertebrates, fish pathogens, plants and algae in the North American Laurentian Great Lakes since the 1880s, which has resulted in the collapse of lake ecosystems and economic hardships (4). In Sweden, the indigenous noble crayfish *Astacus astacus*. has been decimated to one-fifth of its population size in 1907 by the effects of the crayfish plague *Aphanomyces astaci,* the intentional introduction of the American signal crayfish *Pacifastacus leniusculus* and environmental changes (5).

The introduction of alien species has significant socioeconomic consequences for society. Alien species are often intentionally introduced in order to provide new resources or products and to stimulate economic growth. But alien species, both those that are intentionally and unintentionally introduced, have also caused damage to the environment and economically important plants and animals. Costs for eradicating and controlling alien species have been far higher than previously thought. In the United States, the approximately 50 000 alien species cause environmental damages and losses for USD 137 billion annually (6). In the Laurentian Great Lakes, costs for damages caused by the zebra mussel *Dreissena polymorpha* and control measures are estimated to have cost USD 1 billion since 1989 (7). In the Baltic Sea, the introductions of the shipworm *Teredo navalis* and the cladoceran *Cercopagis pengoi*, harmful algae blooms and *Sargassum muticum* have resulted in an economic loss in the Nordic countries of approximately USD 10 million annually (Stephen Gollasch, Institut für Meereskunde, Kiel, pers. comm.). In freshwater environments, no estimates of probable costs and damages have been made. However, a recent court case, in which the Norwegian Ministry of the Environment was found liable for introducing *Mysis relicta* to several lakes and was sentenced by the Norwegian Supreme Court to a fine of USD 640 000 payable to the owners of the water rights (8), illustrates the estimated damage caused by one introduced species.

Since 1800, approximately 50 alien species have been introduced to Swedish lakes and rivers (Fig. 1), of which 35 have established viable populations (8–10). Extensive water regulations and development of large hydroelectric reservoirs from

Box 1. Alien Species

Alien species are species, populations, or genotypes that are moved to an area outside their natural range of distribution with the help of humans. Species or populations, which originate within the political boundaries of a country, but are moved to a new biogeographical region are also alien to their new environment. The vast majority of introductions of alien species into an ecosystem fail. Some introductions survive in the new environment, but fail to establish reproducing populations and are known as incidental or ephemeral. Certain alien species, especially fish such as the rainbow trout and the grass carp are incidental, but through repeated and regular stocking into natural waters are continuously present and may affect indigenous species and ecosystems. In a small number of introductions, an alien species establishes reproducing populations and becomes a permanent member of the local flora or fauna. In time, after 150–200 years, the established alien species may be considered a natural element in the indigenous flora or fauna and is considered naturalized. Of the alien species which become established, a small number may become invasive, i.e. become a threat to indigenous ecosystems, species or gene pools.

The signal crayfish *Pacifastacus leniusculus* has established large populations in the four large Swedish lakes. The Canadian waterweed *Elodea canadensis* is also seen in the background. Photo: I. Lennmark.

Figure 1. Total number of alien species introduced into Mälaren, Vänern, Vättern and Hjälmaren from 1850–2000.

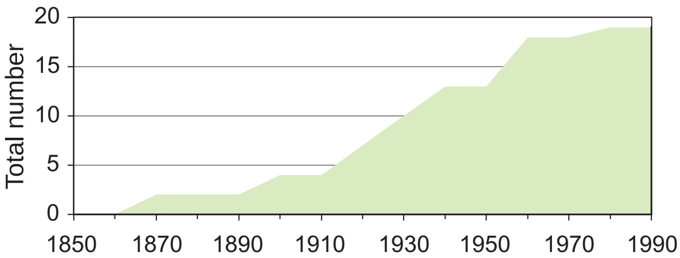
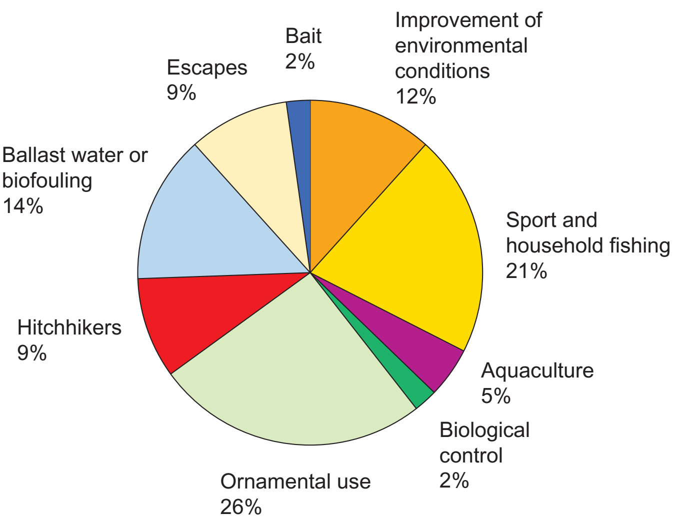


Figure 2. Vectors of introduction for alien species to Swedish inland waters.



1950–1980 have resulted in introductions of alien species and populations of indigenous species from other biogeographical regions in the country, in attempts to reconstruct destroyed food webs and alleviate decreases in indigenous species. The rapid growth of sport fishing and aquaculture has also led to experimentation with stocking with alien species during later decades. Sixty-four established reproducing populations of 4 alien fish species are documented: common carp, brook char, lake char, and cutthroat trout (11).

Introductions to support fisheries are important vectors of introduction, but other vectors have also been important (Fig. 2). In the Swedish large lakes, shipping is an important vector for introduction of alien species through transport of organisms in ballast tanks and through hull fouling. International shipping traffic moves far into the watersystems of Mälaren and Hjälmaren. L. Vänern is connected to L. Vättern and the Baltic Sea through the Göta canal system, and to the Kattegat Sea through the river Götaälv canal system, which is an important commercial shipping route. The Chinese mitten crab, the zebra mussel and the crayfish plague were introduced or spread in these lake systems through commercial shipping and recreational boat traffic (12). Another vector of introduction to the Swedish large lakes is ornamental plants introduced to aquaria or ponds which have spread into the natural environment.

In this article we describe the alien species introduced to the large Swedish lakes and their histories of introduction as known. We then focus on the consequences of the spread of these species and discuss their impact on the ecosystems of the four Swedish large lakes.

ALIEN SPECIES OBSERVED IN THE LAKES MÄLAREN, VÄNERN, VÄTTERN AND HJÄLMAREN

In the four large Swedish lakes about 20 alien species have been observed (Table 1). These include 5 aquatic plants, 6 fish or crayfish species, and 2 fish- or crayfish parasites. One bird, 1 mammal, 1 rotifer and 2 benthic species are also included. Species which occur sporadically are not included in this list. In addi-

Table 1. Year of introduction of alien species to Mälaren, Vänern, Vättern and Hjälmaren (x = introductory year unknown).

	Mälaren	Hjälmaren	Vättern	Vänern
Pathogens and parasites				
Aphanomyces astaci	1907	1908	x	1987
Gyrodactylus salaris	1950	x	x	x
Invertebrates				
Kellicottia bostoniensis	x	1966	1950	
Branchiura sowerbyi	1969			
Dreissena polymorpha	1926	1970		
Eriocheir sinensis	1933			x
Pacifastacus leniusculus	1970	1969	1969	1985
Fish				
Cyprinus carpio	x	x	x	1923
Onchorynchus mykiss	1964	x	1964	1971
Salvelinus namaycush	1964		1973	1963
Salvelinus fontinalis			1973	1963
Birds				
Branta canadensis	x	x	x	1930
Mammals				
Mustela vison	x	x	x	x
Vascular plants				
Acorus calamus	1900	x	x	x
Elodea canadensis	1871	x	x	x
Elodea nuttallii	1991		1970	
Nymphoides peltata	1933			
Ricciocarpus natans	1879	x	x	x
Sum of known introductions	17	12	14	13

tion, the distribution of small organisms which are difficult to identify, e.g. microorganisms like microalgae, bacteria and viruses, are not known.

PATHOGENS AND PARASITES

The crayfish plague, *Aphanomyces astaci* Schicora: The crayfish plague, caused by infection with the fungi *Aphanomyces astaci,* was introduced to Europe from its native North America with imported American crayfish in 1860. It spread rapidly through Europe, decimating an extremely large number of European freshwater noble crayfish. In 1907, the crayfish plague spread to Sweden, when infected crayfish from Finland, imported for human consumption, were thrown into L. Mälaren. The crayfish plague spread rapidly throughout the lake, aided by boat traffic. The subsequent rapid decimation of the substantial crayfish population caused severe economic loss to the local fishing industry. In 1908, the infection attacked Sweden's most fertile stock of the noble crayfish in L. Hjälmaren, where the annual yield amounted to 120 tonnes, which was one-fourth the total production of the noble crayfish in Sweden (13). The crayfish plague spread rapidly to all lakes and streams within the catchment areas of Mälaren and Hjälmaren. Recurrent outbreaks were recorded in the 1920s, 1930s, and 1980s.

The noble crayfish in L. Vättern was not as abundant or economically important as the populations of Mälaren and Hjälmaren prior to the first outbreak of the crayfish plague at the end of the 1930s. A few noble crayfish survived in Vättern until the 1960s, but have since completely disappeared. Lakes and tributaries in the catchment areas of Vänern were infected by crayfish plague in the late 1980s (13).

Humans are the most effective vector for dispersion of the crayfish plague by moving infected fishing equipment and boats, and transplanting fish and crayfish to previously uninfected waters. The crayfish plague is also spread by the natural movements of crayfish, birds, and mammals. The mink has been identified as a vector for spreading the crayfish plague upstream of natural barriers and to previously uninfected waters. Unsuccessful attempts to restore destroyed noble crayfish populations in Mälaren, Hjälmaren, and Vänern through reintroducing noble crayfish failed because of the recurrent outbreaks of the crayfish plague.

The parasitic fluke, *Gyrodactylus salaris* Malmberg: *Gyrodactylus salaris*, a monogenean trematode indigenous to Central Asia, was introduced to Swedish waters in the 1950s with salmon fry or roe imported for aquaculture from the Baltic states. Mortality in Swedish salmon populations in aquaculture when infected with *Gyrodactylus salaris* is about 60%. *Gyrodactylus salaris* spread from Swedish waters to Norwegian aquaculture facilities in 1975 with infected salmon fish or roe and has caused enormous ecological problems, and a 95% mortality rate in the Norwegian wild Atlantic salmon.

INVERTEBRATES

The planktonic rotifer, *Kellicottia bostoniensis* Rousselett: This rotifer is indigenous to North America, but its distribution area has been increased by human activities. *K. bostoniensis* is probably transported in ballast water to Sweden, and was first reported in Swedish waters in 1943 (14). The species occurs mainly in water influenced by pulp-mill effluents and is found in large numbers in the near-bottom water layer, where the oxygen content is fairly low. *K. bostoniensis* is found in the entire L. Mälaren and some of its tributaries. It is also found in some bays of Vänern and Vättern. Its impact on the ecosystem is unknown.

The oligochaete, *Branchiura sowerbyi* Beddard: This benthic tubificid, originally known from Asia, Africa, and Australia, was first observed, in 1969, outside the warm-water effluent of the Västerås Power Plant in L. Mälaren and is still present in the basin. In Europe and North America, *Branchiura sowerbyi* occurs mainly in artificially heated basins. *Branchiura sowerbyi* is by far the biggest oligochaete in the area, ~ 7 cm, but in its natural habitats the species ranges up to 15 cm (15). It has no known impact on the ecosystem.

The zebra mussel, *Dreissena polymorpha* Pallas: The zebra mussel, a native of the Caspian area of Eurasia, has been known from the Baltic Sea since 1800s, and was first observed in L. Mälaren in 1926 (16). *Dreissena polymorpha* is found in the northern and eastern parts of Mälaren and Hjälmaren, as well as in other lakes in central Sweden (17). The zebra mussel has a relatively benign history in Swedish freshwater environments. Its presence has been noted in lakes used by municipal waterworks and industry, but no noticeable damages or fouling problems caused by the zebra mussel are apparent as compared to the major problems seen in the Laurentian Great Lakes. The only negative ecological effect of the zebra mussel observed in Swedish lakes was a decrease in burbot, *Lota lota*, populations in L. Mälaren when zebra mussel populations were at their highest in the 1960s, but this relationship has no statistical significance (13, 18). In L. Mälaren during especially cold winters with thicker than normal ice cover on the lakes, zebra mussels have been observed to die back in substantial numbers. Recolonization after these events is slow (Ted von Proschwitz, Swedish Museum of Natural History, pers. comm.). Perhaps climatic factors hinder the spread of the zebra mussel in Sweden and limit ecological and economic damages.

The Chinese Mitten Crab, *Eriocheir sinensis* Milne-Edwards: The Chinese mitten crab, native to China has spread throughout the world through transport in ballast water. It was first observed in L. Mälaren in

Table 2. Environmental, economic and social effects of alien species in Mälaren, Vänern, Vättern and Hjälmaren, modified after (4). xx = major change, x = minor change.

	Pathogens and parasites	Local extinction of other species	Habitat modification	Competition	Predation	Economic and social effects	Genetic effects
Pathogens and parasites							
Aphanomyces astaci	xx	xx	x			xx	
Gyrodactylus salaris	xx	x				x	
Invertebrates							
Dreissena polymorpha			x	x		x	
Pacifastacus leniusculus	xx	x	x	xx	x	x	x
Fish							
Cyprinus carpio			x				
Onchorynchus mykiss	x			xx	x		
Salvelinus fontinalis				x	x		x
Salvelinus namaycush				x	x		x
Birds							
Branta canadensis	x		x	x			x
Mammals							
Mustela vision		x		xx	xx		
Vascular plants							
Acorus calamus			x	x			
Elodea canadensis			xx	x		x	
Elodea nuttallii			x	x			
Nymphoides peltata			xx	xx		x	

Although the brook char *Salvelinus fontinalis* has been transplanted repeatedly into Vänern and Vättern, it has not established reproducing populations. Photo: I. Lennmark.

1933 (19) and has been reported sporadically also in L. Vänern (13). The Chinese mitten crab is unable to reproduce in freshwater lakes or in the Baltic Sea, as it requires a salt content of at least 15‰ for its eggs to develop. Although unable to reproduce in Swedish waters, it seems to be continually present in low numbers in L. Mälaren due to the large amount of shipping and subsequent release of ballast water. The number of Chinese mitten crabs, about 30 crabs per year are caught in Mälaren, is apparently increasing despite restrictions in the release of ballast water in inland waters. In The Netherlands and Northern Germany, the Chinese mitten crab damages canal banks and road banks through undermining, but such damages have not been reported in Sweden.

The North American signal crayfish, *Pacifastacus leniusculus* Dana: After many failed attempts at restoring the noble crayfish population, Swedish authorities initiated the introduction of an alien crayfish species resistant to the crayfish plague, the North American signal crayfish *Pacifastacus leniusculus.* Since 1969, 40 000–290 000 signal crayfish per year have been released into Swedish lakes and streams. Unfortunately, it was discovered in the 1980s that the signal crayfish, although resistant to the crayfish plague, is often a carrier of the crayfish plague and a source of contagion to the noble crayfish (5).

Repeated stockings of signal crayfish to many locations in L. Hjälmaren 1970–1987 and to L. Vänern and L. Vättern in the 1980s have led to the establishment of a rapidly expanding, successful population and replacement of the noble crayfish. However, stocking with signal crayfish is prohibited in several lakes within L. Vänern's catchment area in order to protect surviving populations of the noble crayfish. In L. Mälaren, stocking with the signal crayfish began in 1970 and continues to this day. In 1993–2000, 40 000–50 000 signal crayfish per year were stocked into L. Mälaren in the vicinity of Stockholm (13).

FISH

The common carp, *Cyprinus carpio* L.: The common carp *Cyprinus carpio* was introduced to Scania, in southern Sweden by Peder Oxe in 1560 for cultivation in ponds for human consumption. Carp is seldom able to reproduce because of the low maximum water temperatures in Swedish waters, but because of its long life-span it has succeeded in maintaining a small but viable population. Reproducing populations of carp are found in the central and western parts of L. Mälaren and near the town of Strängnäs at Mälaren. Carp is also found in Hjälmaren, Vänern, and Vättern, but is extremely rare in L. Vänern (13).

North American Fish Species

The rainbow trout *Oncorhynchus mykiss* Walbaum, native to North America was first introduced to Swedish waters in 1883 for sport fishing. Rainbow trout is stocked into rivers and streams in the catchment areas of Mälaren, Vänern, and Hjälmaren. It is also found in these lakes, but in small numbers. About 10 000 rainbow trout per year were stocked into L. Vättern in 1964 and 1967–1973 and are presently caught relatively often. The rainbow trout is a common put-and-take fish on the western side of Vättern and is raised in aquaculture facilities in the lake. Rainbow trout seldom reproduce in Swedish waters, but have probably established reproducing populations in 2 tributaries to L. Vättern, the rivers Röttleån and Domneån (13).

Lake char *Salvelinus namaycush* Walbaum and brook char *Salvelinus fontinalis* Mitchill, both native to North America, and splake, the hybrid between lake char and brook char, were stocked into Vänern and Vättern in 1963–1973, but have not established reproducing populations (13).

STOCKING OF FISH FROM DIFFERENT BIOGEOGRAPHICAL AREAS IN THE COUNTRY

Fish of native origin, but from different biogeographical areas have also been stocked into L. Vänern, among others *Salvelinus salvelinus* L. from L. Vättern. "Laxing", a hybrid between salmon *Salmo salar* L. and brown trout *Salmo trutta* L. was stocked into L. Vättern in the 1960s, but did not establish reproducing populations. About 40 000 salmon with origins from L. Vänern are transplanted per year into L. Vättern. Another example of a more large-scale put-and-take activity is the periodic release of brown trout and salmon, with origins from the rivers Dalälven and Luleälven in northern Sweden, into the outlet of L. Mälaren. From the outlet of L. Mälaren these stocked species reach the lake. In L. Vänern more than 100 000 individuals of brown trout and salmon smolt were introduced in 1998 and 1999 (13).

BIRDS

The Canada goose, *Branta canadensis* L.: The Canada goose *Branta canadensis* was introduced to Sweden in the 1930s with the transplanting of 5 individuals from a German zoo for the purpose of establishing a population for hunting. Subsequent introductions to other locations in Sweden were made using descendents of these original birds. The Canada goose was introduced to the areas around Hjälmaren and Mälaren in the 1940s, which

The Canada goose *Branta canadensis* since its introduction in the 1930s has grown to a population of 50 000 birds spread throughout Sweden. Photo: E. Andersson.

resulted in the establishment of large populations (20). The Canada goose was observed in the vicinity of L. Vänern in 1930, but nested first in the 1960s. By 1999, the population of the Canada goose in L. Vänern had grown to about 500 (21). The Canada goose is now spread throughout Sweden and had grown to a population of 50 000 by 1990.

MAMMALS

The North American mink, *Mustela vison* Schreber: The North American mink was introduced in the 1920s to Swedish fur farms. Mink began escaping from fur farms almost immediately, but mink populations in the wild became noticeable first after fur farmers deliberately released mink because of food shortages during World War II. Mink populations grew rapidly and mink was soon established throughout Sweden. Mink populations increased rapidly and steadily until the 1990s when, for some unknown reason, a sudden decline began (22). The mink is a superior predator and utilizes land and water environments equally well.

AQUATIC PLANTS

The sweet flag, *Acorus calamus* L.: One of the oldest documented introductions to Swedish lakes and rivers is the sweet flag, introduced to Sweden in the 1600s from the Middle East for use as a spice and medical purposes. *Acorus calamus* propagates vegetatively through rhizome fragments and spreads easily. It was documented as growing in Uppsala in the 1700s and gradually spread along the tributaries to L. Mälaren, reaching the lake at the beginning of the 1900s (23). It has since been reported from all parts of L. Mälaren. Stands of *Acorus calamus* are also found in all the large lakes as well as in many other eutrophic waterbodies in southern Sweden.

The North American waterweeds, *Elodea canadensis* Michx. and *Elodea nuttallii* (Planch.) St John: *Elodea canadensis,* known as the Canada waterweed or Canadian pondweed, was introduced to Europe in 1859 as an aquarium and pond plant in botanical gardens and rapidly spread throughout Europe. *E. canadensis* was first observed in Swedish inland waters in 1874 and is now established in nutrient-rich lakes and slow rivers throughout southern and central Sweden. *E. canadensis* spread into L. Mälaren in the 1890s and grew vigorously in shallow waters in the northern parts of the lake until the 1920s when it decreased and almost disappeared from the first sites of invasion. In the 1950s, *E. canadensis* was found outside the reedbeds in the central parts of L. Mälaren. *E. canadensis* is now integrated into the submerged communities. It behaves as a weed, also in its native habitats in North America, where it develops dense mats that impede water traffic and restrict water recreation (24). It is locally explosive from time to time, but no longer has mass invasions throughout the entire lake, which is contradictory to experiences in L. Baikal and the lakes Jarevatn and Steinsfjord in Norway (25, 26). The low water clarity in L. Mälaren may be a limiting factor. It has also been suggested that *E. canadensis* colonization is initiated and followed by rapid growth in areas where sediment is abundant in iron. Growth is then rapidly terminated, depending on iron reserves and replenishment (24).

Elodea nuttallii, known as the Nuttall waterweed was first observed in the eastern part of L. Mälaren in 1991 (27) and has since been noted at several locations in the northern part of Mälaren. *E. nuttallii,* native to North America, is closely related to *E. canadensis* and grows in shallow water among *Potamogeton*, *Callitriche*, and *Ceratophyllum* on soft bottoms. *E. nuttallii* is apparently rapidly spreading throughout Europe and is outcompeting *E. canadensis* (28). *E. nuttallii* is found in eutrophic, oligo- or mesosaprobic waters with a certain degree of organic pollution (29), while *E. canadensis* has its main distribution in mesotrophic waters. *E. nuttallii* may be able to grow in deeper water than *E. canadensis*. Growth of *E. nuttallii* is stimulated by fertilization with nitrogen and benefits from an excess of N-NH_4^+ (30). Thus, the recently introduced *E. nuttallii* has a potential capacity to increase, if nitrogen concentrations increase in Swedish lakes. Such increases have been reported from The Netherlands where it is partly replacing *E. canadensis* (31).

The fringed water-lily, *Nymphoides peltata* (Gmelin) O. Kuntze: *Nymphoides peltata,* a native of western Siberia, has been repeatedly planted in different waterbodies in the southern and central Sweden since the first introduction in the 1890s. In 1933, a single plant was planted in a lake in the catchment area of the river Arbogaån and by 1975 had spread to cover an area of 0.45 km^2 (32). The beautiful yellow flowers and floating ovate

The fringed water-lily *Nymphoides peltata* has caused extensive problems locally for human recreational use of waters and has displaced indigenous water vegetation through its rapid growth and building of dense stands. Photo: K. Rune, Naturfotograferna.

Predation by the American mink *Mustela vison* threatens ground-nesting birds, the endangered noble crayfish and rare indigenous freshwater mussels. Controlling the spread of mink in Scandinavia is difficult and labor intensive. Photo: L. Mathiasson, Naturfotograferna.

leaves are now found throughout the entire river system of Arbogaån and in L. Mälaren. Attempts to control *Nymphoides* have failed because of its ability to propagate vegetatively, through rhizomes, and roots tightly attached to the sediment. Rhizomes and roots survive mechanical harvesting and rhizome and plant fragments root elsewhere, thus increasing its distribution.

EVALUATING ENVIRONMENTAL AND ECONOMIC CONSEQUENCES OF INTRODUCED SPECIES

The introduction of alien species may have environmental consequences for indigenous species and their habitats. The ecological effects of an introduction may be the alteration of a habitat through physical or chemical processes, disturbance of the natural food web and its processes, increased predation or grazing, and the introduction of new parasites or pathogens (3, 4). Genetic effects of the introduction of an alien species may be hybridization with indigenous species or the selective removal of indigenous organisms through predation or competition, which results in the removal of their adaptations from the gene pool. Another genetic effect may be the loss of reproductive seasons when hybridization fails to produce offspring, which may be critical to acutely threatened species (33). The consequences of these genetic effects are loss of local genetic adaptations and genetic depletion.

Pathogens and Parasites

The greatest environmental effect of the introduction of alien species to the four Swedish large lakes has been the effects of alien pathogens and parasites. Alien pathogens and parasites have also had the greatest socioeconomic impacts because of the consequences for economically important fisheries. The combined effects of the unintentional introduction of the crayfish plague *Aphanomyces astaci* and the intentional introduction of the signal crayfish *Pacifastacus leniusculus* have, together with environmental changes such as acidification of streams and lakes, resulted in a reduction of the population of indigenous noble crayfish *Astacus asctacus* in Sweden to 5% of the population in 1907. The legal and illegal stocking of the signal crayfish, which is often a carrier of the crayfish plague, to waters previously uninfected with the crayfish plague has led to massive outbreaks among noble crayfish and has resulted in a greater distribution of the crayfish plague and the permanent establishment of the plague in certain waters (5). Limiting the distribution of the signal crayfish, as well as actively combating the crayfish plague and restoration of habitats, is necessary to secure the continuing survival of the noble crayfish (34).

Although relatively little is known about the environmental consequences of alien fish species in the four large lakes, it is important to consider their possible effects. Wild rainbow trout is found in small quantities in all of the lakes. Rainbow trout is not included in the National Board of Fisheries' restrictions for transplantation of alien fish species to new waters, as it is considered to be of no great risk because it seldom reproduces. It is, however, known that the rainbow trout is a carrier of the parasite *Gyrodactylus salaris* and may have been an important vector in spreading the parasite to indigenous salmon fish. The widespread practice of stocking rainbow trout may have been instrumental in spreading *Gyrodactylus* thoughout Sweden and Norway (8). Freshwater aquaculture with rainbow trout is now forbidden in Norway because of the risk of infecting wild fish with *Gyrodactylus*. The risks of spreading pathogens and parasites to valuable populations of indigenous salmon fish make the use of rainbow trout in aquaculture in the Vänern and Vättern unsuitable (13).

Competition and Predation

The introduction of the mink *Mustela vison* to the areas around the large lakes has locally affected wildlife negatively through predation and competition and should thus be considered as one of the more problematic alien species. The establishment of mink in the archipelagoes off the Swedish coast and in the large inland lakes in environments previously not affected by large indigenous predators has had negative effects on ground-nesting birds (22, 35) and has resulted in local extinctions. Predation of mink on crayfish and freshwater mussels is significant and contributes to local decreases or extinctions of these organisms (34).

Mink may also affect the threatened populations of the indigenous otter through competition for food and habitats.

The signal crayfish is ecologically and morphologically very similar to the noble crayfish and is a strong competitor with the noble crayfish (36). Initially, the 2 crayfish species can coexist if population densities are low and if the signal crayfish does not carry the crayfish plague. However, if population densities increase, the more aggressive and larger signal crayfish is able to dominate the use of resources, i.e. food, hiding places, spawning sites. The signal crayfish also has a greater rate of population growth as it reaches maturity faster and produces more roe than the noble crayfish (37). The noble crayfish will eventually disappear from waters where signal crayfish are found.

The signal crayfish also has ecological effects on other freshwater species through predation. The predation of the signal crayfish on the roe and fry of the fish *Salvelinus salvelinus* and *Coregonus* spp. may have a negative impact on the populations of these fishes (38). It is also possible that signal crayfish may compete with benthic fish such as ruffe *Gymnocephalus cernuus* L., the burbot *Lota lota* L. and the fourhorn sculpin *Triglopsis quadricornis* L. (13).

The rainbow trout and the brook trout *Salvelinus fontinalis* may compete with indigenous fish, such as the brown trout *Salmo trutta* and the Atlantic salmon *Salmo salar* for habitats and food in running water. Rainbow trout has a faster growth rate than the brown trout and preys upon young brown trout. It is interesting to note that in North America the introduction of rainbow trout has led to extinctions of fish indigenous to the regions such as the cutthroat trout and the Sibling steelhead trout.

Habitat Modification

Alien vascular plants are other introductions with a considerable impact on the water quality of the four large lakes and the recreational use of certain areas in the lakes. Ecological problems caused by plant leaves obstructing subsurface light penetration have appeared in the catchment of L. Mälaren with the introduction of the fringed water lily *Nymphoides peltata*. Similar shading effects are caused by the pondweeds *Elodea canadensis* and *Elodea nuttallii* during phases of rapid growth and mass occurrence. The plants compete with and displace indigenous vegetation, thus reducing biodiversity. The dense stands affect the entire lake ecosystem. *Elodea canadensis* and *Nymphoides peltata* alter the chemical composition of waters by increasing the organic content and contribute to internal fertilization of lakes by taking up nutrients from sediment during the growth phase and releasing them to the water column during decomposition. Both species are able to change the fauna of lakes during periods of mass occurrence. Water birds, especially swans, benefit from the abundant food provided by the growth of *E. canadensis* (8).

The Canada goose affects the natural vegetation communities along shorelines and in shallow water by its intense herbivory. In L. Hjälmaren, Canada geese have grazed the reed-belts along the shoreline since the 1970s. During the 1990s, the grazing intensity of the Canada goose has been so high that the reed community has been affected. In L. Vänern, the size of the reed-belt is said by local residents to have diminished because of the grazing of the Canada goose, but a higher lake water level could also have contributed to the reduction in the reed community.

An ecological effect of the decimation of the noble crayfish has been the accelerated growth of vegetation and the accumulation of organic matter in lakes and streams due to the loss of crayfish grazing (5).

Economic and Social Effects

The disappearance of the noble crayfish after many outbreaks of the crayfish plague has had economic and social effects as well as ecological effects. The disappearance of the rich crayfish fisheries resulted in economic hardship for fishermen and local communities and a need to develop other sources of income. The costs for the attempted restocking of the noble crayfish and the subsequent culture and stocking of signal crayfish has amounted to many millions of Swedish crowns. The Swedes' particular affection for the tradition of festive crayfish parties has led to the import of large amounts of crayfish for consumption from other countries after the disappearance of the indigenous crayfish. The import of more than 2000 tonnes yr^{-1} of Spanish and Turkish mountain crayfish to Sweden in the 1970s and 1980s has contributed to overfishing of these crayfish populations.

The Canada goose *Branta canadensis* is probably ranked as the biggest nuisance of the alien species by sunbathers and swimmers because of the Canada goose's pollution of attractive beaches and parks. Canada goose droppings may pollute swimming water to a degree that is detrimental to human health (39). The Canada goose also has considerable economic impacts through its intense grazing and damage to agricultural crops, especially potatoes, beetroot, and winter crops of wheat, rye, and rape (40).

Elodea canadensis and *Nymphoides peltata* also cause problems for boat traffic, fishing, swimming, and other recreational uses of the lakes where they are present. In L. Mälaren, boat owners complain about scrape damage to boat hulls, when dense stands of *E. canadensis* become heavily encrusted with calcium carbonate, which precipitates in lime-rich waters during periods of intense photosynthesis which raise the pH.

Genetic Effects

Of great importance to the genetic integrity of the four large Swedish lakes is the stocking of indigenous fish species with origins from different biogeographical areas, i.e. alien populations and their consequences for the gene pool of the native fish fauna of the large lakes. In L. Vänern several fish populations indigenous to the region are very seriously threatened by the introduction of trout from other populations. L. Vänern originally contained a number of populations of native brown trout and landlocked Atlantic salmon *Salmo salar* relict to L. Vänern for 9000 years. The regular stocking of populations from different biogeographical areas to compensate for fishery decline due to hydropower developments in the tributaries of L. Vänern resulted in extinction of all but 4 of these relict fish populations, the Atlantic salmon and the brown trout in the rivers Klarälven and Gullspångsälven (13). Populations of the Gullspång salmon and the Gullspång brown trout are considered to be 2 of the most valuable salmonid stocks in Sweden. A conservation program to preserve these populations through artificial breeding and reintroduction has had problems with loss of genetic variation due to improper handling of the brood stocks, but satisfactory results are now being attained (41).

CONCLUSIONS

Despite the relatively large number of introductions to Swedish waters the ecological consequences of these introductions have not been considered especially significant, with the exception of the introduction of the crayfish plague. Ecosystem collapses like those which have occurred in the Laurentian Great Lakes and L. Baikal are not known from Swedish waters. Ecosystems that are vulnerable to damage from invasive alien species have earlier been considered to be those which are species-poor with few trophic levels (42, 43). Although the four Swedish large lakes from an international perspective are considered species-poor and have few trophic levels, the expected ecosystem damages have not occurred, even for invasive alien species which have caused much damage in other countries with similar climatic and geological conditions. However, introductions of alien species and populations may cause local problems of considerable dignity.

This may indicate that the effects of species diversity on the invasibility of lakes in Sweden are complex and dependent on interactions between the different indigenous species, interactions between indigenous species and ecological factors as well as between indigenous species and alien species (1, 44).

The few examples of ecosystem damage from alien species: the effects of the signal crayfish and the transplanted indigenous fish species with origin from different biogeographical areas to L. Vänern, have followed major changes in the ecosystem which were detrimental to indigenous species and opened new ecological niches to the alien species. The disappearance of the noble crayfish enabled the signal crayfish to rapidly establish large populations as there was no competition. The regulation of L. Vänern for hydropower led to an altered hydrological regime and construction of barriers, which hindered reproduction of the indigenous brown trout and relict Atlantic salmon. The new competition situation with alien populations which were better adapted to the new hydrological regime was a secondary factor which nonetheless hastened the demise of the indigenous populations.

It is also possible that the ecological problems caused by alien species in Sweden have been masked by the more obvious and very serious environmental problems caused by acidification, eutrophication, and general pollution of waters, as well as physical destruction of habitats. Both intentional and unintentional introduction and establishment of alien species often follow anthropogenic changes in the environment. These changes are often of such magnitude that ecosystems are altered significantly. Ecological effects of alien species which are introduced to these altered ecosystems are difficult, if not impossible, to separate from effects of the original anthropogenic ecosystem alteration. Thus, this "biological pollution" caused by the introduction of alien species is seen as just one of many factors which cause harm to ecosystems. This is seen in the decline of the endangered *Alisma wahlenbergii*, in which eutrophication and water regulation are given as the primary causes, but increased competition from *Elodea* and the zebra mussel may have also contributed to its decline (45).

It is evident, that we lack basic knowledge of what ecological effects and consequences alien species have in Swedish waters and that research and regional cooperation is necessary in order to achieve this understanding.

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