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Invasion pressure on the Finnish Lake District: invasion corridors and barriers

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Abstract

In a literature-based study, 29 non-indigenous species present in northeastern European waters were assessed for their potential for introduction and establishment in Finnish inland lakes. Their physiological and ecological demands were compared to abiotic and biotic lake conditions. The availability of adequate vectors was surveyed from shipping statistics for the Saimaa Canal, which connects the Finnish Lake District to the Baltic Sea. There exists a high probability for the introduction of six non-indigenous invertebrate species, i.e., *Anguillicola crassus*, *Potamothrix heuscheri*, *Potamothrix vejdovskyi*, *Hemimysis anomala*, *Cercopagis pengoi* and *Gmelinoides fasciatus*, with the Gulf of Finland as the main donor area. Barriers against new species introductions, which maintain the biological integrity of Finnish inland lakes, include low water temperature, northern isolated location, and low concentration of nutrients and major ions.

Introduction

Flora and fauna have colonised the Nordic inland waters for the last 10,000 years, and the natural immigration of organisms can be regarded as an ongoing post-glacial process. Meanwhile, the anthropogenic introduction of alien species has increased during the last two centuries, resulting in problems and concerns worldwide. The brackish Baltic Sea (including the Kattegat) has received about 100 non-indigenous species (NIS), of which ∼ 70 have been able to establish reproducing populations in some sub-regions (for further details, visit the Baltic Sea Alien Species Database 2003). Of these, 20 species are considered harmful. Aquatic invasive species inevitably affect biodiversity by adding new functions to the ecosystem, by altering prevailing ecosystem functions or by competing with and even replacing native species. Although some benefits of alien species exist (e.g., pelagic larvae function as food for commercial fish; species of interest for hunting and fisheries), these do not outweigh the adverse impacts of invasive NIS. The economic impacts of invasives include, e.g., fouling of power plants, underwater constructions and ship hulls, causing preventive measures (e.g., the use of the toxic antifouling ingredient tributyltin), as well as harmful algal blooms, which affect fisheries and tourism (Leppäkoski 2002).

Ballast water transport is considered to be the main vector for marine and brackish-water NIS introductions to new areas (Carlton 1985; Carlton and Geller 1993; Olenin et al. 2000; Ruiz et al. 2000; Minchin and Gollasch 2002). Since the 1880s, ships have used ballast water to increase stability on voyages (Carlton and Geller 1993). The ballast water capacity is about 25% of a ship's dead weight (Locke et al. 1993) and it has been calculated that at any time between 3000–7000 species are transferred with ballast water worldwide (Carlton and Geller 1993; Carlton 1999; Gollasch et al. 2000a, b).

The concept of 'guilty until proven innocent' is central when predicting future introductions and invasions

(Ruesink et al. 1995). A species' invasion capacity is not a characteristic, but proof of a match between the species' ecophysiological demands and environmental conditions in the recipient area, along with the availability of proper vectors for transport. Any given species can therefore become invasive at the right time and place, with adverse effects, which are seldom reversible or even controllable. The aquatic environment is a complex system where several factors influence each other at different levels and times. The prediction of possible impacts of NIS in the recipient area is therefore not included in this study, since it cannot be assumed that species behave in same way even if climatic, hydrographical and ecological conditions change. By predicting the identity of future invaders our knowledge of the risks associated to invasive NIS is clarified and can function as a tool in adequate risk assessment, impact analysis and management (Ricciardi and Rasmussen 1998).

This study is an assessment of the invasion potential of 29 non-indigenous aquatic species in the Finnish Lake District, which is connected to the Baltic Sea via the Saimaa Canal. These species were selected because of their occurrence in adjacent waters (i.e., the Baltic Sea, as well as lakes and rivers of the Baltic countries Estonia, Latvia and Lithuania and northwestern Russia) and because they are known as successful invaders. Our study includes a vector analysis based on shipping statistics. Similar evaluations have already been performed, e.g., for some Nordic coastal ports (Gollasch and Leppäkoski 1999), for the northeastern Canadian lakes (Whittier et al. 1995), for the North American Great Lakes (Ricciardi and Rasmussen 1998; MacIsaac et al. 2001; Kolar and Lodge 2002; Grigorovich et al. 2003) and for Australian marine waters (Hayes and Sliwa 2003). By comparison, no similar studies are known for European inland waters.

The Finnish Lake District

Finland has about 56,000 lakes (>1 ha). The oldest lakes, situated in the southeastern parts of the country were formed post-glacially, ~ 10,000 years ago, and form a continuous interconnected waterbody, called the Saimaa area (10,460 km^2) or the Finnish Lake District (Figure 1). Other lakes in Finland are mostly separated from each other and the coast, and are mainly located in the south and west.

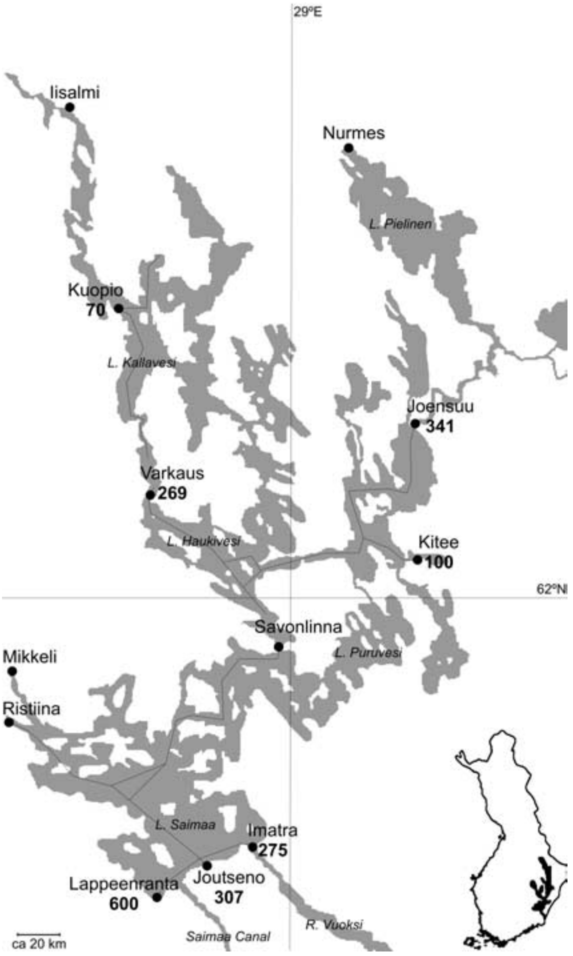

Figure 1. The Saimaa area and its deep-water channels and total shipping cargo exchange in some of the inland ports in 2001 in 1000 tonnes (other inland ports about 155,000 tonnes in all). The fairways (and the Saimaa Canal) are allowed for ships with maximum length of 82.5 m, breadth 12.6 m, depth 4.4 m and height (over water-level) 24.5 m (Finnish Maritime Administration 2003).

Chemistry, hydrography and biology

Finnish inland lakes, being geologically and ecologically young, do not host any endemic species (Särkkä 1996). Due to the nutrient-poor bedrock, they lack both the buffering capacity and resistance to acidification and eutrophication. They are naturally acidic due to humic substances that originate from wetlands and woods giving the oligotrophic waters a characteristic, brown colour. Humus also serves as additional fuel for detritus-based food webs.

The lakes in the southern and central parts of Finland are the most phosphorus- and nitrogen-loaded,

Table 1. The lake water quality in different parts of Finland (the Saimaa area is marked in grey) (Mannio et al. 1998).

Area	Total P [$\mu g\,l^{-1}$]	Total N [$\mu g\,l^{-1}$]	BC* [$\mu ekv\,l^{-1}$]	Alkalinity [$\mu ekv\,l^{-1}$]	SO_4 [$\mu ekv\,l^{-1}$]	pH	TOC [$mg\,l^{-1}$]	Colour [$mg\,Pt\,l^{-1}$]
SE Finland	22	680	439	150	167	6.3	13.6	100
S Saimaa area	14	530	358	170	119	6.6	9.3	70
N Saimaa area	15	560	311	140	82	6.7	10	80
NE Saimaa area	15	380	187	50	51	6.1	7.8	80
C Finland	42	800	283	90	61	6.4	13.6	140
W Finland	22	540	206	80	43	6.5	13.4	160
N Finland	4	210	218	140	44	7	4	25
Finland, whole	13	410	241	120	58	6.6	7.7	60

*Ca + Mg + Na + K.

a consequence of local urbanisation and agriculture (Mannio et al. 1998; Table 1). Typically, the calcium content of inland lakes is about 3 $mg\,l^{-1}$ (range 2.1–4.4 $mg\,l^{-1}$ in an oligotrophic forest lake in a natural state in central Finland), with a pH of 6–7 (Kirjavainen and Westman 1999). By comparison, lakes on the Åland Islands in the northern Baltic Sea are surrounded by a calcium-rich bedrock, giving pH values up to 9. The calcium content in these lakes is around 25 $mg\,l^{-1}$ but can reach 65 $mg\,l^{-1}$ (Carlsson 2000). In the Saimaa area, the sodium content is 2.2–2.5 $mg\,l^{-1}$, with a maximum in the polluted southern parts where concentration can rise up to 10 $mg\,l^{-1}$. Finland's northern latitude affects water temperature. In the Saimaa area, the long-term (1961–1990) mean temperature increased from 16.1 °C in June to 18.3 °C in August and decreased to 13.8 °C in September (Atlas of Finland 1993).

Boreal lakes, surrounded mainly by coniferous forests and bogs, offer a demanding chemical and physical environment for aquatic organisms. The flora and fauna of Finnish inland lakes are a mixture of glacial relicts (e.g., the ringed seal of Lake Saimaa, *Phoca hispida saimensis* (Nordq.) and freshwater populations of smelt *Osmerus eperlanus* L.), and species invaded later or introduced by man. Evolution has formed a species-poor native flora and fauna that is well adapted to the natural acidity and low alkalinity in the lakes. Many ecofunctional types are absent and the number of keystone species is low (Kokko and Kaijomaa 1985; Toivonen 1985), resulting in simple food webs.

Around 20 alien species are now permanent inhabitants of the Finnish inland lakes, of which half were introduced intentionally. The crayfish plague (*Aphanomyces astaci* Schikora), the signal crayfish (*Pacifastacus leniusculus* Dana) as a carrier of that plague, and the Canadian waterweed (*Elodea canadensis* L.C. Rich.) are three species that have caused negative impacts on these lakes (Ulvinen and Varkki 1999; Westman 2000). Some introduced fish species are of economic importance in the Saimaa area, e.g., *Salvelinus fontinalis* Mitchill and *Onchorhyncus mykiss* (Walbaum) (Urho et al. 1995). The Chinese mitten crab (*Eriocheir sinensis* (Milne-Edwards)), has recently reached the Saimaa area (Silfverberg 1999) and is therefore included in this evaluation. The New Zealand mud snail (*Potamopyrgus antipodarum* (Gray)) has been found in newly isolated coastal lakes on the Åland Islands since the 1970s (Carlsson 2000), but has not been recorded in Finnish mainland lakes.

Invasion corridors, vectors and barriers

The Saimaa Canal

The Saimaa area has a long history of both shipping and tourism. In 1856, the Lake District was connected to the Baltic Sea (the easternmost part of the Gulf of Finland) via this Canal. Today the canal measures 43 km in length, of which about half is on Russian territory. The canal is the only gateway to Finnish inland ports, which mainly serve as export terminals of forest industry products such as wood pulp and paper. Increasing trends in commercial traffic in European waterways are given in the Saimaa Canal shipping and passenger traffic statistics (Figure 2).

Hot-spot mapping

The main vector of NIS to the Finnish Lake District is shipping, including ballast water transport and biofouling on hulls. Ballast water intake is accomplished in port areas and fouling is impossible when a ship is moving faster than 2 $m\,s^{-1}$ (Schloesser 1995), therefore

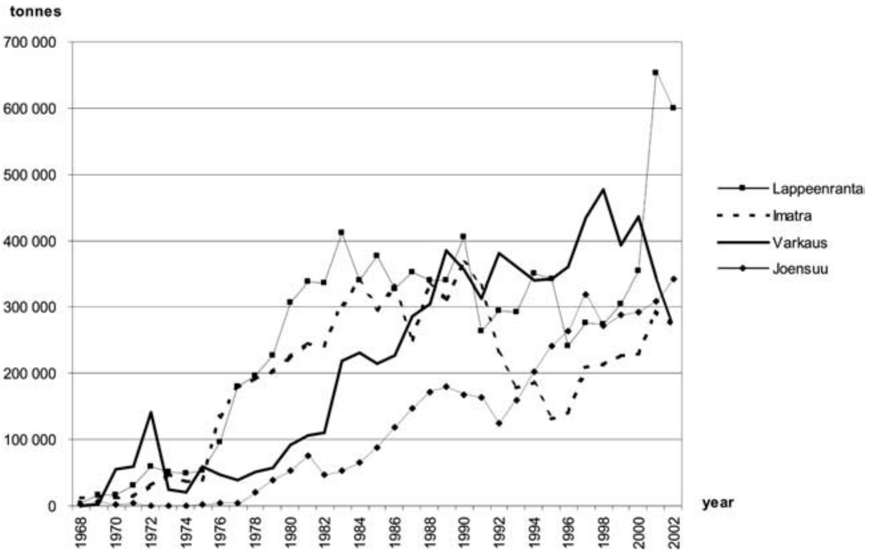

Figure 2. Amount of cargo transported via the Saimaa Canal handled in the largest Finnish inland ports during 1968–2002 (Finnish Maritime Administration 2003).

ports are the bridgeheads ('hot-spots') for alien species introductions. The survival of species during ballast water transport is dependent on the duration of the voyage and a species' capability to sustain prevailing circumstances in the ballast water tanks (Gollasch et al. 2000a, b). The shorter the trip, the greater the species survival and the probability of a successful introduction (Gollasch et al. 2000a). The origin of the ballast water and the shipping route are therefore important when mapping hot-spot areas and potential species. Shipping to the Finnish Lake District and its adjacent areas is increasing every year. Ships arrive mainly from ports located in the northern Baltic Sea, but also from the southern Baltic and North Sea coasts (Figures 3A and B). The Gulf of Finland is a special area for the study of bioinvasions, because the salinity gradient from 0 to 6 PSU allows both fresh- and brackish-water NIS to establish reproducing populations, enhancing a successful secondary introduction into adjacent water bodies. The process of ballast water introductions to the Saimaa area is reviewed in Figure 4.

Additional vectors include birds and semi-aquatic mammals (biovectors), fishing gear or aquaculture (live food trade, aquarium trade) and unintentional release or escapes (Minchin and Gollasch 2002). Introductions to Finnish lakes with these rather unpredictable vectors are possible, especially to the coastal, enclosed lakes in southern and western Finland.

Barriers – biological integrity

The biological integrity of a system reflects its original, natural conditions, where all kind of human interference has been and is absent. Karr (1993) and Cairns (1995) define biological integrity as a system's capability to support and maintain a balanced complexity even when faced with disturbance from outside. Biological integrity can thus be measured by comparing prevailing circumstances to the conditions that could be expected without any anthropogenic influence. The biological integrity of the Finnish Lake District is based on three main characteristics: low temperature, low nutrient level and isolation.

Blacklisted species

An environmental matching approach, where several factors are observed and compared, has been used in this study (Figure 5). Using literature studies, species of fresh- or brackish-water origin were examined for their physiological demands (salinity range, temperature tolerance, nutritional needs and reproductive demands) and ecology (grazing/predation, interference with other species, reproduction capacity in different communities). The invasion histories of these species were also examined: origin, invasion corridors and possible vectors, distribution (including a list of where the

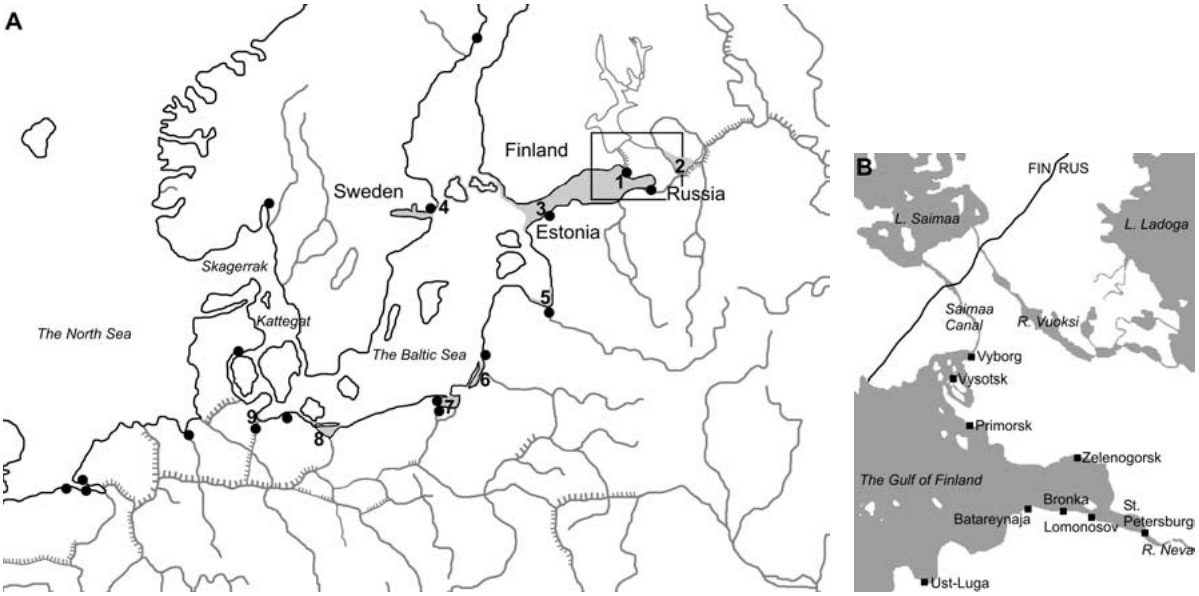

Figure 3. The potential donor areas (in grey) of NIS to the Finnish Lake District; areas combined with the highest risk are first in the list: 1 = The eastern part of the Gulf of Finland, including the Neva estuary outside of St. Petersburg; 2 = Neva River–Lake Ladoga system; 3 = Middle and western parts of the Gulf of Finland including both the southern and northern coasts; 4 = Archipelago Sea between Finland and Sweden, including the gateway to the Swedish Lake District; 5 = Gulf of Riga; 6 = Curonian Lagoon; 7 = Vistula Lagoon; 8 = Szczecin Lagoon; 9 = Kiel Bight. The black circles indicate the main north European ports from where ships are calling Finnish inland ports (A). The easternmost part of the Gulf of Finland, the boxes indicate Russian oil terminals and ports (B) (Finnish Maritime Administration 1993–2000).

species have not been able to establish themselves) and impact on the recipient area. This information was annexed with shipping statistics for the Saimaa Canal and with the prevailing chemical and physical conditions in the Finnish Lake District in order to predict future biological invaders to the area.

Of the 29 species examined, 13 turned out to have no or only a weak capacity for introduction and establishment in the Saimaa area due to unsuitable environmental requirements with local climatic conditions and/or a lack of suitable vectors. An intermediate capacity was recognised in 10 species, while the 6 species most likely to be introduced and established in the Finnish Lake District in the near future were identified. These blacklisted species have a physiology that fits with the conditions in the lakes and their distribution covers possible invasion corridors and vector lines to the area.

Anguillicola crassus (Kuwahara, Niimi and Itagaki). The swim bladder nematode, which is a blood-sucking limnetic parasite, is native to southeastern Asia but has spread to most parts of the world with imported eels. Today, it lives both in fresh- and brackish-waters in all Nordic countries, except Finland (Höglund and Thulin 1994), though it was found in 11 eels ascending three rivers in western Finland in 2001 (Tulonen 2002). The species has many characteristics typical of a successful invader: rapid spread, a resistant larval stage, high fecundity and ability to spread with a variety of hosts, and its life cycle is completed in the swim bladder of adult eels. Infection can cause swim bladder necrosis, decreased growth, orientation disturbances and increased mortality for the host eel, leading to reproduction failure and economic losses for eel culture and fisheries (Tulonen 2002). Invasion corridors to Finnish lakes are numerous (i.e., via Swedish and other Baltic coastal lakes, and the Gulf of Finland), as well as geographically close. The eel, a natural vector, is native to Finnish inland waters, although continuously maintained with intentional introductions of imported eel populations. One possible barrier might be low water temperature since the eel stops eating at temperatures less than 10 °C. This prevents the transfer of *A. crassus* larvae from ingested copepods to the swim bladder of the eel (Höglund and Thulin 1994).

Potamothrix heuscheri (Bretscher) and *P. vejdovskyi* (Hrabe). These two tubificid oligochaetes are of Ponto-Caspian origin (the Black and Caspian Seas, the Sea of Azov and their catchment areas). *P. heuscheri*

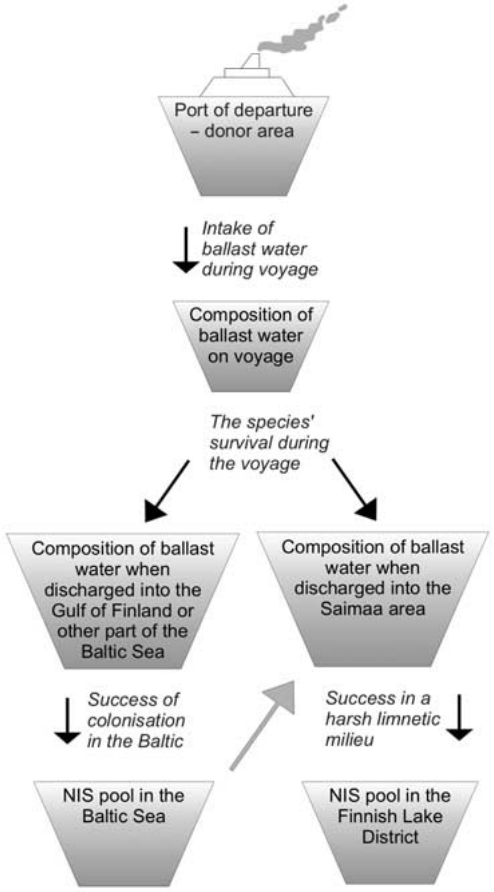

Figure 4. The critical stages in imaginary ballast-borne introductions to the Finnish Lake District; each stage represents a different environment and the species that will become established in the recipient area have to be able to adjust to all these stages. The grey arrow indicates secondary introductions from the Baltic Sea to the Finnish Lake District (including all stages of ballast water introduction). Modified from Hayes (1998, 2002).

has extended its range to Europe, Africa and South America. It is found in all countries bordering the Baltic Sea; in Finland it is found among the benthic fauna of the Gulfs of Finland and Bothnia (Milbrink 1999). Both species tolerate even anoxic conditions and typically invade ecologically stressed communities.

An introduction of these two oligochaetes into the Finnish Lake District is highly possible, both by shipping and biovectors. The native species *P. hammoniensis* (Mich.) indicates eutrophy and lives in nutrient-rich lakes in the Saimaa area (Nurmi 1998). This species shares its habitat with *P. heuscheri* and *P. vejdovskyi* in the Swedish Lake Mälaren (Milbrink 1980), indicating an overlap in their ecological and physiological requirements. Therefore, the probability of establishment of these two species in Finnish inland lakes is also high.

Cercopagis pengoi (Ostroumov). This predatory cladoceran is of Ponto-Caspian origin. It has been spread, probably with ballast water, to the Baltic Sea and the North American Great Lakes, the Baltic Sea being apparently the donor region (Cristescu et al. 2001). The species has high reproduction capacity and is tolerant of temperatures as low as 8 °C in the Baltic Sea. A dormant egg stage enables survival in harsh conditions, e.g., under ice cover in winter (Telesh and Ojaveer 2002). Different life stages of *C. pengoi* can be easily transported with ballast water, biovectors and fishing gear. A mass occurrence of the species forms jelly-like lumps on nets and other equipment and due to clogging of fishing nets, *C. pengoi* has caused economic losses for some fishing companies in the easternmost Gulf of Finland (Panov et al. 2002). Moreover, due to a considerable dietary overlap of *C. pengoi* and planktivorous fish (herring and sprat), a high population density of *C. pengoi* can also result in a decline of food resources for these important commercial fish (Telesh and Ojaveer 2002). On the other hand, *Cercopagis* may locally constitute an important portion of the diet of herring, stickleback and smelt (Antsulevich and Välipakka 2000). The possibility for the species to be established in the Finnish Lake District is high. No barriers are present, invasion corridors are short and vectors are available.

Gmelinoides fasciatus Stebb. This limnetic amphipod, endemic to Lake Baikal, has extended its range through successful intentional introductions in 1971–1975 to European inland waters, including several lakes in the Baltic Sea drainage basin, e.g., on the Karelian Isthmus. Accidental introduction of *G. fasciatus* into Lake Peipsi has resulted in occurrence of the species in the whole littoral zone of the lake. In 1999, it was recorded for the first time in the easternmost parts of the Gulf of Finland (Panov and Berezina 2002).

G. fasciatus is adapted to a wide range of temperature and other environmental factors. The benthic gammarid is an aggressive invader in both Lake Ladoga and Neva Bay, where it has replaced the native species, *Gammarus lacustris* Sars (Panov and Berezina 2002). Macroinvertebrates such as gammarid amphipods can affect prey abundance more than large predators like fish (Dick and Platvoet 1996; MacNeil and Prenter 2000). However, one limitation for the species'

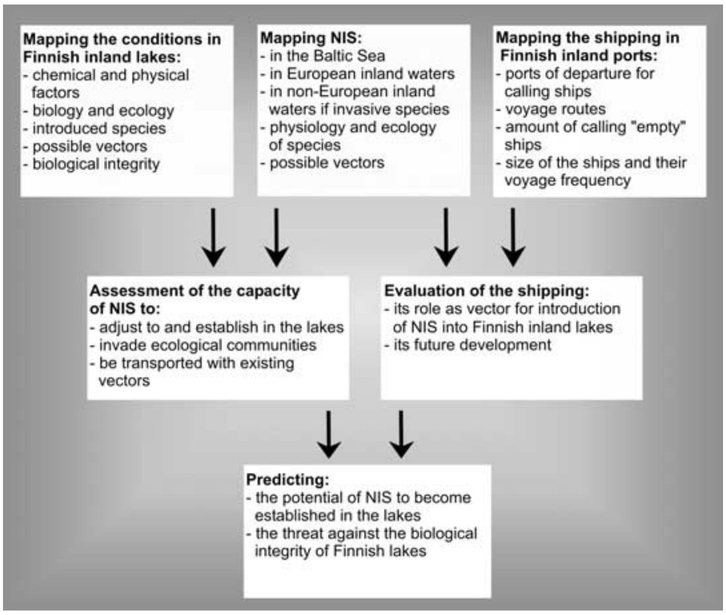

Figure 5. Assessment of the probability of NIS to become established in the Finnish Lake District – the work protocol.

establishment in Finnish inland lakes may be the low calcium concentration, because *G. fasciatus* requires a calcium content of $> 5\,\mathrm{mg\,l^{-1}}$ and $\mathrm{pH} > 6$ (Panov and Berezina 2002). Nevertheless, the introduction of *G. fasciatus* by ballast water from the Neva estuary to Finnish inland lakes and an adaptation to the local environment remains probable.

Hemimysis anomala G.O. Sars. This Ponto-Caspian mysid was intentionally introduced into some lakes in the former Baltic republics of the USSR in the early 1960s, to improve food availability for fish. This has resulted in vast unintentional secondary introductions to new areas via shipping (Salemaa and Hietalahti 1993), and today the species is found along the whole southern and southwestern coast of Finland and in the Stockholm archipelago (Leppäkoski and Olenin 2000; Leppäkoski et al. 2002). *H. anomala* is a brackish-water species, but it can also adjust to limnetic waters (Kelleher et al. 1999). The species is a top-down regulator of the plankton community, and can affect planktivorous fish populations and whole food webs negatively (Salemaa and Hietalahti 1993). Vectors and invasion corridors are available for a successful introduction into the Finnish Lake District, while barriers are missing.

The results from this assessment have been summarised in Table 2. Species were classified into four groups according to their probability of becoming established in Finnish inland lakes. Blacklisted species and their characteristics are listed separately in Table 3.

Discussion

Finnish inland lakes offer a harsh environment for introduced species, because their high acidity, low alkalinity, low temperature and low nutrient level are obstacles for most species. Nevertheless, it is important to remember that all environments are patchy and some microhabitats may be suitable for species that could not otherwise survive in an average Finnish lake.

The scale of the risk and threat of alien species introductions to the biological integrity of aquatic environments is hard to determine since any ecological risk assessment includes many unknown and uncertain factors. After the evaluation, changes in prevailing conditions were recognised as the main threat, when considering the establishment probability of invasive NIS. These changes could result in both intracontinental (the Ponto-Caspian faunal element, e.g., *P. heuscheri*, *Pontogammarus robustoides* (G.O. Sars) and the round goby *Neogobius melanostomus* Pallas), as well as intercontinental invasions (the North American contribution, e.g., *Gammarus tigrinus* Sexton), in the future.

By providing non-native species with easier and more efficient invasion corridors to the Finnish Lake

Table 2. The species included in the assessment and their probability to be introduced or become established in the Finnish Lake District (the blacklisted species are marked in grey). Areas mentioned for invasion history are BS = the Baltic Sea, BSP = Baltic Sea proper, GoF = Gulf of Finland and GL = Great Lakes of North America. Possible impacts: C = competition (with native species) for food or space, HA = habitat alteration, F = fish food, A = influence on human activity. Risk groups: 0 = no, 1 = low, 2 = intermediate and 3 = high probability to be introduced and become established in the Finnish Lake District.

	Species	Origin	Salinity range, PSU (optimum)	Temperature range, °C (optimum)	Invasion history	Invasion barriers	Vectors	Possible effects	Risk group	References
Dinophyceae	*Prorocentrum minimum*	Marine cosmopolite	0.7–35 (15–35)	8–36 (18–26)	S. BS 1980s, GoF 1993	Insufficient nutrition, low salinity	Ballast sediment, ballast water	C, A	1	[1, 2]
Magnoliophyta	*Nymphoides peltata*	Ponto–Caspian	0	>7	Eurasia, inland lakes in SWE	Low temperature, low alkalinity, long distance	Biovectors (birds), ballast sediment, ballast water	C, A	1	[3, 4]
Nematoda	*Anguillicola crassus*	SE Asia	0–10 (0)	>10	Italy 1982, N. Europe 1985, SWE 1987, Finland 2001	Low temperature	Import of infected eels, biovectors (hosts), ballast water	C, A	3	[5–7]
Polychaeta	*Hypania invalida*	Ponto–Caspian	0	?	German rivers and canals 1958, Moscow River 1993	Long distance, low temperature	Ballast sediment, ballast water, biovectors	C, HA, F	2	[8, 9]
Oligochaeta	*Potamothrix heuscheri*	Ponto–Caspian	0–?	?	Europe, Africa, S. America; L. Mälaren in SWE 1915–1916; GoF 1969	Oligotrophy	Ballast sediment, ballast water, biovectors	C, HA	3	[10–12]
Oligochaeta	*Potamothrix vejdovskyi*	Ponto–Caspian	0–?	?	Europe, Africa, S. America; L. Mälaren in SWE, GoF	Oligotrophy	Ballast sediment, ballast water, biovectors	C, HA	3	[10, 13, 14]
Oligochaeta	*Branchiura sowerbyi*	Japan, E Asia	0	10–30 (25)	N. America; German rivers and canals 1959, L. Mälaren in SWE 1970	Low temperature, oligotrophy	Ballast sediment, ballast water	C, HA	1	[10, 15–17]
Hydrozoa	*Cordylophora caspia*	Cosmopolite	0.5–(5–7)	(21–33)	BS end of 1800; GoF	Insufficient nutrition, low salinity	Ship hulls	HA, A	1	[18–20]
Gastropoda	*Potamopyrgus antipodarum*	New Zealand	0–26 (0)	<28	Europe (Thames) 1859, W. BS 1887, German rivers and canals 1900, Finland (Åland) 1926, N. America 1990	Low calcium content	Ship hulls, ballast water, wandering, biovectors	C, F, A	1	[17, 21–24]
Bivalvia	*Dreissena polymorpha*	Ponto–Caspian	0–7	−1.5–32 (12–24)	Europe (Great Britain and Germany) 1824, L. Mälaren in SWE 1926, GoF 1980s, GL 1988	Low pH, low calcium content	Ship hulls, ballast water, biovectors	C, HA, A	0	[17, 20, 25–27]

Bivalvia	*Dreissena bugensis*	Ponto–Caspian	Lower than *D. polymorpha*	Lower than *D. polymorpha*	GL 1989	Long distance, no/distant vectors	Ship hulls, ballast water, biovectors	C, HA, A	1	[28, 29]
Bivalvia	*Corbicula fluminea*	SE Asia, Africa, Australia	0–14 (0–5)	2–34 (15–16)	USA in early 1900s, German rivers and canals 1980s	Long distance, no/distant vectors, low temperature	Ship hulls, ballast water, biovectors	C, HA, A	1	[17, 30]
Cladocera	*Cercopagis pengoi*	Ponto–Caspian	0–15	8–20 (16–20)	GoF 1992, BSP 1994–1997, GL 1998	Low temperature	Ballast water, fishery equipment, biovectors	C, F, A	3	[31–33]
Calanoida	*Acartia tonsa*	American Atlantic/ Indopacific	0–22	0–29.5	English Channel and BS 1920s, BSP 1925, GoF 1939	Irregular vectors, low salinity, low temperature	Ballast water	F	0	[34–37]
Cirripedia	*Balanus improvisus*	N. America	>1.5	Eurythermal	BS 1844, SW Finland 1860s, Black Sea 1899, Caspian Sea 1976	Low salinity	Ship hulls, ballast water, biovectors	HA, A	0	[6, 20, 38]
Decapoda	*Eriocheir sinensis*	E. Asia	Catadromous	0–?	Europe (Germany) 1912, BS 1926, Finnish coast 1933, N. BS 1950, Saimaa area 1999	Reproduction not possible in limnetic water	Ballast water, wandering	C, HA, A	2*	[20, 26, 39, 40]
Amphipoda	*Corophium curvispinum*	Ponto–Caspian	0–15	(12–20)	S.E. BS 1930s, German rivers and canals 1987	Low sodium content, low temperature	Ballast water	C, HA, F	1	[20, 41, 42]
Amphipoda	*Gmelinoides fasciatus*	Lake Baikal	0–2	0.2–32	European inland waters 1960s**, Lake Ladoga 1996, GoF 1999	Low calcium content	Ballast water, biovectors, wandering	C, F	3	[41, 43]
Amphipoda	*Obesogammarus crassus*	Ponto–Caspian	0–14	?	European/Russian inland waters 1960s–1970s**, Curonian Lagoon 1962, Vistula Lagoon 1999	Long distance, irregular vectors	Ballast water, biovectors, wandering	C, F	2	[41, 44–46]
Amphipoda	*Pontogammarus robustoides*	Ponto–Caspian	0–14	?	European/Russian inland waters 1960s–1970s** (incl. Curonian Lagoon), GoF 1999, Szcecin and Vistula Lagoon 1990s	Low calcium content	Ballast water, biovectors, wandering	C, F	2	[41, 44–47]
Amphipoda	*Chaetogammarus ischnus*	Ponto–Caspian	0–14	?	Poland 1928, European/ Russian inland waters 1960s–1970s**, Curonian Lagoon 1962, Germany 1978, GL 1995	Long distance, irregular vectors	Ballast water, biovectors, wandering	C, F	2	[41, 44–46, 48]
Amphipoda	*Chaetogammarus warpachowskyi*	Ponto–Caspian	0–10	?	European/Russian inland waters 1960s–1970s**, Curonian Lagoon 1962	Long distance, irregular vectors	Ballast water, biovectors, wandering	C, F	2	[41,44–46]

Table 2. *Continued.*

	Species	Origin	Salinity range, PSU (optimum)	Temperature range, °C (optimum)	Invasion history	Invasion barriers	Vectors	Possible effects	Risk group	References
Amphipoda	*Gammarus tigrinus*	N. America	0–?	?	S BS 1975, Odra 1992, Szczecin Lagoon 1990s, Vistula Lagoon 1998	Long distance, irregular vectors	Ballast water, biovectors, wandering	C, F	2	[14, 17, 41, 49, 50]
Amphipoda	*Dikerogammarus haemobaphes*	Ponto–Caspian	0–8	6–30	European/Russian inland waters 1960s–1970s**, Moscow River 1996, Vistula River 1997, Vistula Lagoon 2000s, lower Odra 2000s	Long distance, irregular vectors	Ballast water, biovectors, wandering	C, F	1	[41, 45, 46, 51]
Amphipoda	*Dikerogammarus villosus*	Ponto–Caspian	0–20	0–20	German rivers and canals 1990s, Elbe 1998, lower Odra 2000s	Long distance, irregular vectors	Ballast water, biovectors, wandering	C, F	1	[17, 46, 51, 52]
Mysida	*Hemimysis anomala*	Ponto–Caspian	0–19	?	European/Russian inland waters 1950s–1960s**, BS (S.W. Finland) 1992, GoF, The Netherlands 1997	No known barriers	Ballast water, biovectors	HA	3	[38, 44, 51, 53, 54]
Mysida	*Paramysis lacustris*	Ponto–Caspian	0–10	0–32.5 (7–28)	European/Russian inland waters 1950s–1970s**, Curonian Lagoon 1962	Long distance, low temperature	Ballast water	C, HA, F	2	[45, 55, 56]
Pisces	*Neogobius melanostomus*	Ponto–Caspian	0–37	(18–19)	Gulf of Gdansk 1990, Gulf of Riga 2002	Low temperature	Ballast water, wandering	C, F, A	2	[57–59]
Pisces	*Perccottus glenii*	Amur River basin	0–?	0–30 (15–20)	St. Petersburg 1916, GoF 1953–1954; Vistula River 1996–1997	Unknown	Aquaria	A, F	2	[60–62]

*Non-reproductive pseudopopulations only.

**Intentional introductions.

1 = Grzebyk and Berland (1996), 2 = Hajdu et al. (2000), 3 = Cook (1990), 4 = Mossberg and Stenberg (2003), 5 = Höglund and Thulin (1994), 6 = Weidema (2000), 7 = Tulonen (2002), 8 = Tittizer (1998), 9 = Slynko et al. (2002), 10 = Milbrink (1980), 11 = Milbrink (1999), 12 = Rieradevall and Real (1994), 13 = NIES (2002), 14 = Baltic Sea Alien Species Database (2003), 15 = Bonacina et al. (1994), 16 = Xiaosong and Matisoff (1997), 17 = Tittizer et al. (2000), 18 = Arndt (1984), 19 = Jansson (1994), 20 = Olenin and Leppäkoski (1999), 21 = Lassen (1978), 22 = Økland (1990), 23 = Carlsson (2000), 24 = Mackie (2000), 25 = Mackie and Schloesser (1996), 26 = Gollasch et al. (1999), 27 = Josefsson and Andersson (2001), 28 = Claxton and Mackie (1998), 29 = Orlova et al. (1998), 30 = McMahon (2000), 31 = Panov et al. (1999), 32 = Gorokhova et al. (2000), 33 = Leppäkoski (2001), 34 = Lindquist (1959), 35 = Cervetto et al. (1999), 36 = Kurashova (2003), 37 = Leppäkoski et al. (2002), 38 = Leppäkoski and Olenin (2000), 39 = Silfverberg (1999), 40 = Valovirta and Eronen (2000), 41 = Jazdzewski (1980), 42 = Van den Brink et al. (1993), 43 = Panov and Berezina (2002), 44 = Birshtein et al. (1968), 45 = Arbaciauskas (2002), 46 = Jazdzewski and Konopacka (2002), 47 = Berezina and Panov (2003), 48 = Witt et al. (1997), 49 = Gruszka (1999), 50 = Jazdzewski and Konopacka (1999), 51 = Bij de Vaate et al. (2002), 52 = Bruijs et al. (2001), 53 = Salemaa and Hietalahti (1993), 54 = Ketelaars et al. (1999), 55 = Khmeleva and Baichrov (1987), 56 = Razinkovas (1997), 57 = Jude (1997), 58 = Skora (2001), 59 = H. Ojaveer, Estonian Marine Institute, pers. comm., 60 = Diripasko (1997), 61 = Terlecki and Palka (1999), 62 = Froese and Pauly (2002).

Table 3. Matching of the characteristics of the most probable invaders to the Finnish Lake District and the environmental conditions in the area.

	Vector availability	Matching salinity	Matching temperature	Matching pH/Ca	Resistant life stages	Barriers
Anguillicola crassus	+++	+++	+	+++	+++	+
Potamothrix heuscheri	+++	+++	+++	+++	+++	+
Potamothrix vejdovskyi	+++	+++	+++	+++	+++	+
Hemimysis anomala	+++	+++	++	+++	++	+
Cercopagis pengoi	+++	+++	+++	+++	+++	+
Gmelinoides fasciatus	+++	+++	+++	++	+	+

+ = low; ++ = intermediate/good; +++ = high.

District, the barrier of isolation becomes eroded and biological integrity is weakened. This is already happening via increasing shipping to adjacent areas, e.g., Primorsk, St. Petersburg and other shipping centres in the eastern Gulf of Finland, some of which are awaiting financial and legal approval for expansion (Rytkönen et al. 2002a, b). Similarly, shipping statistics for the Saimaa Canal also show an increasing trend, which means larger ballast water volumes in the Finnish Lake District.

In December 2001, the Russian oil terminal Primorsk was officially opened to transport Siberian oil to different parts of Europe and other continents. During the first operational year, about 12 million tons of crude oil were transported from Primorsk via the Baltic Sea (Rytkönen et al. 2002a, b). This amount is estimated to increase to about 40 million tons per year in 2005 (K. Jolma, Finnish Environment Institute, pers. comm.). For the Gulf of Finland, the most important transit area for secondary introductions into the Lake District, the total amount of oil carried has been estimated at 100 million tons per year already by 2004–2005 (Panov et al. 2002). This increases the amount of ballast water transported into the area while large oil tankers call at Primorsk and other oil terminals with no or little cargo on board. Russian crude oil is shipped mainly to fresh- or brackish-water ports in northwestern Europe and both native species and NIS present in these ports are likely to be transferred to the northern Baltic by oil tankers.

Some of the species with low or intermediate potential could still be successfully introduced if the proper vectors were available, e.g., the bivalves *Dreissena bugensis* Andr. and *Corbicula fluminea* (O.F. Müller), which have the capability to tolerate conditions in Finnish inland lakes. *D. bugensis* is found in the Rybinsk Reservoir along the Black/Caspian Sea-Volga-Baltic invasion corridor since 1997 (Slynko et al. 2002) and *C. fluminea* has been even more successful than *D. polymorpha* in European inland waterways, occurring as far north as the River Odra, Poland (Tittizer et al. 2000).

The state of pollution in the Finnish Lake District and surrounding areas is another central question when assessing the probability of NIS being introduced into the area. The barrier of limited nutrition availability in Finnish inland waters can be broken by eutrophication. Emissions from the forest industry, agricultural runoff and other sources of diffuse loading, as well as the discharge of pollutants from shipping, can all add nutrients and other chemicals to the environment, thereby threatening biological integrity.

The barrier of low temperature is the third element of the biological integrity of the Finnish Lake District. Low temperature restricts most of the species likely to invade the Finnish inland lakes. A rise in mean world temperature by 1.0 °C–3.5 °C has been predicted for the next century. This has consequences for aquatic introductions to areas in the northern hemisphere, where the duration of ice cover in lakes, rain/snow ratio, runoff, etc., are determined by atmospheric temperature. Consequently, global warming could be the final blow to the biological integrity of Finnish inland lakes.

Panov et al. (1999) and Slynko et al. (2002) forecast an increased number of introductions into areas in the northern hemisphere with rising global temperature. There are a number of Ponto-Caspian species that have recently expanded their distribution along the Black Sea–Baltic Sea invasion corridor. Several of them can be expected to arrive in the eastern Gulf of Finland in the future and, consequently, form a pool of potential invaders to the Finnish Lake District. Slynko et al. (2002) claim that the mean water temperature of the Rybinsk Reservoir in the Volga waterway corridor has increased from 12 °C to 15 °C since the 1960s. During the same period, the amount of non-native Ponto-Caspian, sub-tropical and tropical species has increased, and some of them have become naturalised in the area. Among the newcomers in the Volga-Baltic corridor there are southern vascular plants (e.g., *Lemna gibba* L., *Vallisneria spiralis* (Tiger), *Phragmites altissimus* (Benth.) and *Typha laxmannii* (Lepech.)), cladocerans (e.g., *Cornigerius m. maeoticus* (Pengo) and *Podonevadne trigona* (Sars) ssp. *ovum*), copepods (e.g., *Heterocope caspia* Sars and *Calanipeda aquaedulcis* Kritsch.) (Panov et al. 1999; Slynko et al. 2002) and gastropods (e.g., *Lithoglypus naticoides* (Pfeiffer)). Among fish species, the Amur sleeper *Perccottus glenii* Dybowski, an escapee from aquaria, is already a permanent member of the fish fauna in the Neva estuary (Panov et al. 2002), but seems to be restricted by some barrier from further spread to the Baltic Sea and inland lakes.

The low pH and calcium content of Finnish lake water are not easily changed and serve as 'gatekeepers' against certain species (especially molluscs) even when the barriers of distance, lack of nutrients and temperature are removed. The Ponto-Caspian gammarid *P. robustoides* is one of the several amphipods that have been intentionally introduced to European limnetic waters in order to enhance fish production. Secondary introductions have expanded the geographical range of the species (Jazdzewski 1980; Arbaciauskas 2002). In the coastal Baltic Sea, *P. robustoides* is the most widespread alien gammarid, occurring in the southern and southeastern coastal lagoons and in the eastern Gulf of Finland (Jazdzewski and Konopacka 2002; Berezina and Panov 2003). The species is tolerant to a wide range of temperature, salinity and current velocities (Jazdzewski 1980; Tittizer et al. 2000) and occurs at the mouth of an open and short invasion corridor to the Saimaa area. Nevertheless, the barrier of low concentration of major ions seems to restrict the species' establishment in certain parts of the Neva estuary (N.A. Berezina, Russian Academy of Sciences, pers. comm.), which is why the probability of an establishment of *P. robustoides* in the Finnish Lake District stays at intermediate level.

A comparison of this work with similar studies (Ricciardi and Rasmussen 1998; MacIsaac et al. 2001; Grigorovich et al. 2003) shows that the blacklisted species are similar for two distant areas, i.e., the Great Lakes of North America and the Finnish Lake District. The amount of non-native species in both areas, including species' exchange between them, is also increasing with time. The future prospects in invasion ecology for the Finnish Lake District are similar to the rest of the world's enclosed and semi-enclosed aquatic ecosystems. The introduction of NIS, invasive or not, will increase, as will their impacts on diversity of our biota. To manage the problem with invasive NIS, we have to work in a preventive manner, develop mechanisms that can minimise introductions and try to reduce, but still accept, the uncertainty that is a companion of any risk assessment.

Predictive analyses of potential future invaders, including their possible effects on a recipient area, can be accomplished with the help of literature, experiments and models (Ricciardi and Rasmussen 1998). Kolar and Lodge (2002) stressed the importance of developing quantitative models for assessing the risks of alien species and proposed that it is possible to conduct detailed risk assessments for specific areas and species. Other preventive methods in stopping the stowaways of seas and lakes include ballast water treatment, international agreements and regulations. Large-scale work has to be undertaken, since any deterioration of the biological integrity in, e.g., the Baltic Sea, can be reflected by similar changes in the Saimaa area and other adjacent waters.

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