



Exotic species in Lake Champlain

J. Ellen Marsden^{a,*}, Michael Hauser^{b,1}

^a Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington VT 05405, USA

^b Vermont Department of Environmental Conservation, Water Quality Division, Waterbury VT 05671, USA

ARTICLE INFO

Article history:

Received 9 July 2008

Accepted 27 January 2009

Communicated by David Barton

Index words:

Invasion vector

Canals

Lake Champlain

Great Lakes

Exotic

ABSTRACT

The Lake Champlain basin contains substantially fewer exotic species ($N = 48$) than the Great Lakes ($N > 180$), in part due to its isolation from commercial traffic. Exotic species have been introduced by authorized and unauthorized stocking, bait buckets, use of ornamental plants, and through the Champlain and Chambly canals that link the lake to the Hudson River, Mohawk River, Erie Canal, and the Great Lakes. Several species, such as water chestnut and zebra mussels, have had severe ecological, economic, and nuisance effects. The rate of appearance of new species increased in the 1990s, potentially as a result of increasing activity in the basin, improved water quality in the Champlain Canal, and increased sampling. Efforts to slow the introduction of new species have focused on public education and legislation to reduce bait bucket introductions and quarantine undesirable plants; however, the major remaining vector for introductions is the Champlain Canal. An estimated 20 species have entered the lake via canals, of which at least 12 used the Champlain Canal, and numerous species in the connected drainage systems could still enter via this route; some are already in the Erie Canal. Most recently (2008), the Asian clam was discovered two locks below Lake Champlain. The Lake Champlain canals also function as a conduit for exotic species exchange between the Hudson River, St. Lawrence River, and Great Lakes. The potential for future introductions could be reduced by a biological barrier on the Champlain Canal, and additional emphasis on public education.

© 2009 Elsevier Inc. All rights reserved.

Introduction

The invasion of North American aquatic ecosystems by non-indigenous or exotic species has been occurring at least since Europeans first began to settle the continent, and possibly prior to that time. While a few early invaders, such as carp (*Cyprinus carpio*), sea lamprey (*Petromyzon marinus*), and the Asian clam (*Corbicula fluminea*) received considerable attention as nuisance species, it was the invasion of zebra mussels (*Dreissena polymorpha*) into the Laurentian Great Lakes in the late 1980s that brought the problem of aquatic nuisance species (ANS) to the widespread attention of the public and policy-makers. The Nonindigenous Aquatic Nuisance Species Prevention and Control Act of 1990, re-authorized as the National Invasive Species Act in 1996 and the National Aquatic Invasive Species Act in 2007, brought resources to bear on the problem of ANS. Mills et al. (1993) documented 139 non-indigenous species (NIS) in the Great Lakes alone, and 113 NIS in the Hudson River (Mills et al., 1996). Considerable effort has been expended in research and public education aimed at understanding the vectors of introduction and spread of ANS, and preventing further introductions, as illustrated

by the creation of organizations such as the Great Lakes Panel on Aquatic Nuisance Species, Great Lakes Aquatic Nonindigenous Species Information System (NOAA), and Sea Grant's National Aquatic Nuisance Species Clearinghouse (NOAA), among others.

Lake Champlain, bordered by New York, Vermont, and Quebec, has been invaded by a diversity of species that have entered the lake by several different vectors (Table 1). Some of these species have and continue to cause substantial problems that are costly to the states and to local businesses and homeowners; notable among these nuisances are Eurasian watermilfoil (*Myriophyllum spicatum*), water chestnut (*Trapa natans*), and zebra mussels. The purpose of this paper is to document the exotic aquatic species in the Lake Champlain basin and their probable vectors of introduction, with a brief discussion of strategies to reduce future invasions.

Methods

We use herein the term 'exotic' to denote species that are not native to the Champlain basin and have been introduced to the basin as a consequence of human activities such as stocking, accidental releases, and the linking of isolated drainages via construction of canals. Introduced species do not always become established or self-sustaining; we identify, below, species that do not appear to be reproducing in the basin. We recognize that this exotic species inventory may not be comprehensive. We can be reasonably certain that the lists of fish and plant species are complete, as both these

* Corresponding author.

E-mail addresses: ellen.marsden@uvm.edu (J.E. Marsden), mikeh@firsttreks.com (M. Hauser).

¹ Current address: 449 Beech Hill Rd., Stowe, VT 05672, 802-253-6081.

groups are well-studied and their biogeography is reasonably well understood. Due to the paucity of historic and even current synoptic surveys of lower taxa, however, the lists of macroinvertebrates and plankton are likely far from complete; groups such as benthic meiofauna, protozoans, and most microbes are entirely unstudied.

We have included in this document only species for which we can be reasonably certain of their status as exotics, for example, European and Asian species that clearly arrived in the basin through human influences. Species whose status is controversial are listed separately, and include species such as redbfin pickerel (*Esox americanus americanus*), which various authors list as exotic or native based on their specimens or interpretation of likely zoogeographic patterns of movement. Sea lamprey (*P. marinus*), which recent genetic studies suggest is native to lakes Champlain and Ontario (Waldman et al., 2004; Bryan et al., 2005), is included in this list because of the absence of any historical mention of sea lamprey wounding on native fishes; opponents of the concept that they may be native note that the genetic data do not provide proof, but rather a weight of evidence that suggests the Lake Champlain population has been isolated for several thousand years. We also rely on the expertise of other authors who have done extensive zoogeographical reviews of various taxa (e.g., Countryman, 1978; Smith, 1985a; Jokinen, 1992; Carlson and Daniels, 2004; Langdon et al., 2006) or invasions (Mills et al., 1993, 1996; de Lafontaine and Costan, 2002; Strayer, 2006).

The presence of several species in Lake Champlain has been recorded only in agency reports or collections; for example, the first tench (*Tinca tinca*) found in the basin was caught by a University of Vermont graduate student in 2002, but the finding was not reported in the primary literature. Therefore, this paper serves as the formal record of the following exotic species in the Lake Champlain watershed (Table 1): gizzard shad (*Dorosoma cepedianum*), blueback herring (*Alosa aestivalis*), alewife (*Alosa pseudoharengus*), tench, rudd (*Scardinius erythrophthalmus*), big-ear radix (*Radix auricularia*), woodland pondsnail (*Stagnicola catascopium*), Chinese mystery snail (*Cipangopaludina/Bellamya chinensis*), rusty crayfish (*Orconectes rusticus*), obscure crayfish (*Orconectes obscurus*), northern pike lymphosarcoma, and largemouth bass virus.

The pathways by which species were introduced are also difficult to identify. With the exception of deliberate introductions, such as fish stocked by state or federal agencies, the route of introduction of a species into a new watershed must be inferred from probabilities. Thus, we indicate the few cases in which the vector is known, and for others give the line of reasoning that suggests a most likely pathway for introduction. Several species may have been introduced by a combination of vectors, such as species initially brought into the region as bait or for culture and then further spread through canals.

Geography of Lake Champlain and connected waters

Lake Champlain is a 193 km long, narrow lake bounded by Vermont on the east, New York on the west and south, and Quebec on the north (Fig. 1). The lake flows from Whitehall in the south to its outlet, the Richelieu River, at the north end. Habitats in the lake vary widely; the south lake is eutrophic and essentially riverine, the main lake, with a maximum depth of 122 m, is meso- to oligotrophic, Mallets Bay and the Northeast Arm are mesotrophic, and Missisquoi Bay in the northeast is eutrophic. The lake is naturally connected to the St. Lawrence River via the Richelieu River, below all natural barriers to the Atlantic Ocean.

Aquatic species currently have natural access to Lake Champlain only from the north end via the Richelieu River in Quebec (Fig. 2). The Richelieu River is 115 km long with an average discharge of 271 m³/s. Historically, passage of species through the river may have been limited by the rapids between St. Jean sur Richelieu and Chambly, which drop

the river through an elevation of 24 m; when the level of Lake Champlain is low, usually in summer, much of the rapids have very low water volume and velocity. However, in 1843 the Chambly Canal was opened to bypass 20 km of rapids on the Richelieu River, and may facilitate passage of organisms up the river (Fig. 2). A dam was constructed in 1846 at Saint-Ours and historically blocked fish passage; a fish bypass was completed on this dam in 1911 but ceased to function in 1967 when the dam was rebuilt. A new vertical slit ladder bypass was installed by 2001, with a primary focus of allowing passage of Canadian endangered species such as the copper redhorse (*Moxostoma hubbsi*). The dam at Saint-Ours is bypassed by the Saint-Ours canal, built in 1849; the single lock drops the water 1.5 m (McKibben and McKibben, 1997). A second dam was built at Chambly in 1896, 52 km upstream; the dam had a fish passage, which was not replaced when the dam was repaired between 1965 and 1969 (Verdon et al., 2003). Eel ladders were installed on both dams between 1998 and 2001, and plans are underway to improve fish passage at these barriers.

Lake Champlain is currently connected to other watersheds via a system of canals. The Champlain Canal, first opened in 1823 at the south end of the lake, links Lake Champlain directly to the Hudson and Mohawk Rivers (Fig. 2). In 1825 the opening of the Erie Canal linked Lake Champlain, via the Champlain Canal, to the Great Lakes, Oneida Lake, and Finger Lakes. The Chambly Canal improves the water linkage to the St. Lawrence River and Atlantic Ocean. We consider the Champlain Canal to be the more important vector for exotic species transfers, because the Chambly Canal does not create a new aquatic connection into Lake Champlain. However, since the construction of the dams, movement of species through the Richelieu River likely involves passage through the canal, and species transfer is likely facilitated by boat traffic in the canal.

Zoogeography of Lake Champlain

Prior to the influence of humans, the fauna of Lake Champlain was established after the retreat of the Wisconsin glacier 8000–13,500 years ago. The glacier largely eliminated aquatic fauna from the Champlain Valley; as it receded, recolonization occurred from refugia that were temporarily connected to the basin (Langdon et al., 2006). From 13,000 to 12,000 years ago, ice dams created Lake Vermont in the Hudson Valley, with connections to the precursor of Lake Ontario. By 12,000 a connection to the Atlantic Ocean in the north created the Champlain Sea and allowed saltwater fauna to enter. Overall, eastern and southern fauna entered from the unglaciated Atlantic Coastal Refugia, and western species entered from the Mississippian Refugium, via the Mohawk and St. Lawrence valleys, from both the north and south ends of the Champlain Valley. This western linkage supplied Lake Champlain with a higher diversity of fishes (79 native species), mussels (17 native species), and other macroinvertebrates than is found elsewhere in New England (Fichtel and Smith, 1995; Langdon et al., 2006). Lake Champlain therefore shares much of its fauna with the Great Lakes, St. Lawrence River, and Hudson/Mohawk River drainages, complicating the identification of species as recent invaders versus post-glacial colonists.

Historic changes in the Lake Champlain ecosystem structure

The historic (and present) coldwater food web in Lake Champlain is surprisingly simple compared with the adjoining Great Lakes. Prior to the 20th century, the coldwater food web in Lake Champlain apparently supported, as in Lake Ontario, three native piscivores: lake trout (*Salvelinus namaycush*), Atlantic salmon (*Salmo salar*), and burbot (*Lota lota*). Their prey base, and that of the coolwater walleye (*Sander vitreus*), must have been largely composed of rainbow smelt (*Osmerus mordax*), with some component of coregonids (*Coregonus* spp.), sculpins (*Cottus* spp.), and possibly emerald shiners (*Notropis atherinoides*). The broad forage base of coregonid species present in

Table 1
Exotic species in Lake Champlain.

Taxon/Common name	Latin name	Native range	Source	Vector	Date	Information
Plants						
Lythraceae						
*Purple loosestrife	<i>Lythrum salicaria</i>	Europe, Asia	NY State Barge Canal	Champlain Canal	<1929	Muenschler, 1930a
Haloragaceae						
*Eurasian water milfoil	<i>Myriophyllum spicatum</i>	Europe, Asia, Africa	Washington DC	Unknown	1962	Countryman, 1978
Trapaceae						
*Water chestnut	<i>Trapa natans</i>	Europe, Asia, Africa	Mohawk, Hudson	Champlain Canal	1940s	Countryman, 1970
Butomaceae						
*Flowering rush	<i>Butomus umbellatus</i>	Europe, Asia	St. Lawrence	Canals?	1928	Countryman, 1978
Hydrocharitaceae						
European frog's bit	<i>Hydrocharis morsus-ranae</i>	Europe, Asia	Richelieu R.	Canals	1993	Countryman, 1978
Iridaceae						
Yellow flag iris	<i>Iris pseudacorus</i>	Europe, Africa, Med.	NE US	Stocked (u)	1904	Eggleston, 1904
Poaceae						
*Common or giant reed	<i>Phragmites australis</i>	Europe	New York	Unknown	Unknown	Saltonstall, 2002
Menyanthaceae						
Yellow floating heart	<i>Nymphoides peltata</i>	Europe	New York	Champlain Canal?	1950s	Countryman, 1978
Potamogetonaceae						
Curly leaf pondweed	<i>Potamogeton crispus</i>	Eur., Asia, Africa, Aust.	Widespread	Unknown	1929	Muenschler, 1930a
Najadaceae						
Slender-leaved naiad	<i>Najas minor</i>	Europe, Asia	Hudson R.	Canal?	2002	Mills et al., 1993
Brassicaceae						
Great water cress	<i>Rorippa amphibia</i>	Europe	MA, Quebec	Unknown	1929	Marie-Victorin, 1964
Alismataceae						
Water plantain	<i>Alisma gramineum</i>	Europe, western US	Unknown	Unknown	1961	Countryman, 1978
Gomphonemataceae						
Didymo	<i>Didymosphenia geminata</i>	Europe, Asia, Canada	Unknown	Accidental	2008	VTDEC
Fish						
Salmonidae						
Rainbow trout	<i>Oncorhynchus mykiss</i>	Pacific northwest	Hatcheries	Stocked (d)	1972	VTDFW
Brown trout	<i>Salmo trutta</i>	Europe	Hatcheries	Stocked (d)	1980	VTDFW
Cyprinidae						
Goldfish ^a	<i>Carassius auratus</i>	Asia	Aquarium trade	Aquaria	Unknown	Langdon et al., 2006
*Common carp	<i>Cyprinus carpio</i>	Asia	Great Lakes, Hudson	Canals, stocked (u)	1929	Greeley, 1930
European rudd	<i>Scardinius erythrophthalmus</i>	Europe	Unknown	Bait	1991	C. McKenzie VTDFW
*Tench	<i>Tinca tinca</i>	Europe	Upper Richelieu	Stocked (u)	2002	Vachon and Dumont, 2000, authors
Clupeidae						
Gizzard shad	<i>Dorosoma cepedianum</i>	N. America, widespread	Hudson	Champlain Canal	1993	C. McKenzie VTDFW
*Blueback herring	<i>Alosa aestivalis</i>	N. US Atlantic coast	Hudson	Champlain Canal	1976–78	VTDFW
*Alewife	<i>Alosa pseudoharengus</i>	Atlantic coast, L. Ontario	Unknown	Stocked (u)	2003	B. Pientka VTDFW
Atherinidae						
Brook silverside	<i>Labidesthes sicculus</i>	Hudson/St. L.	Hudson/St. L.	Canals	1998	Marsden et al., 2000
Ictaluridae						
*Black bullhead ^a	<i>Ameiurus melas</i>	N. America, widespread	Unknown	Stocked (u)	<1987	Carlson and Daniels, 2004
Centrarchidae						
Largemouth bass	<i>Micropterus salmoides</i>	Great Lakes, Miss. R.	Unknown	Canals, stocked (u)	<1900	Carlson and Daniels, 2004; Smith, 1985b
Black crappie	<i>Pomoxis nigromaculatus</i>	St. Lawrence watershed	St. Lawrence R.	Stocked (u)	<1930	Carlson and Daniels, 2004
White crappie	<i>Pomoxis annularis</i>	western New York	New York	Stocked (u)	Unknown	Langdon et al., 2006
Moronidae						
*White perch	<i>Morone americana</i>	Atlantic drainages	Hudson	Champlain Canal	1984	Plosila and Nashett, 1990
Molluscs						
Bithyniidae						
*Faucet snail, mud bithynia	<i>Bithynia tentaculata</i>	Eurasia	Unknown	Champlain Canal	late 1800s	Fiske and Levey, 1996
Lymnaeidae						
Big-ear radix	<i>Radix auricularia</i>	Eurasia	Hudson, St. L.	Stocked? (u)	1999	P. Stangel, VTDEC
Woodland pondsnail	<i>Stagnicola catascopium</i>	New England, Great Lakes	Erie Canal	Champlain Canal	<1994	VTDEC
Hydrobiidae						
Buffalo pebblesnail	<i>Gillia altilis</i>	Atlantic drainage	Erie Canal	Champlain Canal	<1993	Jokinen, 1992, Brown et al., 1993
Pleuroceridae						
Sharp hornsnailed	<i>Pleurocera acuta</i>	New York	Erie Canal	Champlain Canal	Unknown	Jokinen, 1992
Viviparidae						
Chinese mystery snail	<i>Bellamya (Cipangopaludina) chinensis</i>	Asia	Lake Erie	Stocked (u)	2003	VTDEC
Banded mystery snail	<i>Viviparus georgianus</i>	SE Canada to Florida	Erie Canal	Champlain Canal	<1988	Jokinen, 1992, VTDEC
Valvatidae						
European stream valvata	<i>Valvata piscinalis</i>	Eurasia	Oneida L., Hudson	Unknown	<1972	Mills et al., 1993
Dreissenidae						
*Zebra mussel	<i>Dreissena polymorpha</i>	Eurasia	Europe	Champlain Canal	1993	M Toomey, pers. comm.; Soper, 1993

Table 1 (continued)

Taxon/Common name	Latin name	Native range	Source	Vector	Date	Information
Sphaeriidae						
European fingernail clam	<i>Sphaerium corneum</i>	Eurasia	Unknown	Unknown	<1972	Burch, 1972; Mills et al., 1993, VTDEC
Greater European pea clam	<i>Pisidium amnicum</i>	Eurasia, Africa	Great Lakes, St. L. Genesee, Hudson R	Unknown	<1972	Burch, 1972, Mills et al., 1996; Fiske and Levey, 1996
Crustaceans						
Cambaridae						
*Rusty crayfish	<i>Orconectes rusticus</i>	Ohio River basin	Connecticut R.	Bait	1994	VTDEC
Allegheny crayfish	<i>Orconectes obscurus</i>	New York to Virginia	central New York	Bait	1988	VTDEC
Big water crayfish	<i>Cambarus robustus</i>	Ontario, midwest, south	Ontario, NY	Bait	<1957	Crocker, 1957
Bosminidae						
Water flea	<i>Eubosmina coregoni</i>	Europe	Great Lakes	Canals	<1991	Benson, 1999
Cyclopidae						
Cyclopoid copepod	<i>Thermocyclops crassus</i>	Eurasia, Africa	Eurasia, Africa	Unknown	<1991	Duchovnay et al., 1992
Other invertebrates						
Coelenterata						
Freshwater jellyfish	<i>Craspedacusta sowerbyi</i>	Asia	Lake Erie	Unknown	1995	M. Ferguson VTDEC
Turbellaria						
Vortex worm	<i>Dugesia lugubris</i> / <i>Schmidtea polychroa</i>	Europe	St. Lawrence	Chambly Canal	<1968	Ball, 1969
Pathogens						
*Muskellunge and northern pike lymphosarcoma		N. America	New York	Accidental	2002	T. Jones VTDFW
Largemouth bass virus		Southern US	Unknown	Unknown	2002	T. Jones VTDFW

Asterisks identify species that are nuisances in Lake Champlain or elsewhere. Source indicates closest range to Lake Champlain prior to arrival in the lake. Date indicates first sighting of the species in the Lake Champlain watershed. Authorized stocking of fish is noted as stocked (d); stocked (u) includes organisms brought into the basin deliberately but without authorization. VTDEC: Vermont Department of Environmental Conservation, VTDFW: Vermont Department of Fish and Wildlife.

^a Presumed not self-sustaining in the basin, but have appeared in more than one survey over time.

the Great Lakes is restricted in Lake Champlain to only two species, lake whitefish (*Coregonus clupeaformis*) and cisco, or lake herring (*C. artedii*). *Mysis relicta*, a critical element of the coregonid diet, is abundant in Lake Champlain, but *Diporeia (Pontoporeia) affinis*, abundant until recently in the benthos of the Great Lakes, is scarce in the main lake (Bell, 1971; Myer and Gruending, 1979). Atlantic salmon numbers declined with the construction of dams until their complete disappearance from the lake by 1852 (Smith, 1985b); in contrast, causes for the extirpation of lake trout from the lake by 1900 are not known. Stocking of salmonids — lake trout, rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and Atlantic salmon — was intermittent prior to the 1970s, when an annual stocking program was implemented. All four salmonids and walleye depend primarily on smelt for forage; the current diet of burbot has not been described.

Dams and other anthropogenic changes in the lake's watershed, such as logging, farming, and limited industry, were also responsible for the decline of lake sturgeon (*Acipenser fulvescens*). American eel (*Anguilla rostrata*) outmigration from the lake began to decline precipitously in the late 1980s to early 1990s; this decline may be related in part to the removal of fish passages from dams on the Richelieu River at Saint-Ours and Chambly in the 1960s (Verdon et al., 2003). Restoration of salmonid fisheries was impeded by parasitism by sea lamprey; sea lamprey control began experimentally in 1990 and a long-term control program began in 2003 (Marsden et al., 2003).

Biological surveys of Lake Champlain

Historic biological data for Lake Champlain are sparse. The earliest document dedicated to Vermont was Zaddock Thompson's *Natural History of Vermont*, published in 1854. Thompson recorded the fish, molluscs, and crayfish of Lake Champlain, but with sufficient gaps (less than 65% of the currently known fish species are named) that the information is of limited value. In the same era, DeKay (1842) provided extensive information about Lake Champlain fauna in his survey of New York. The largest comprehensive survey of the aquatic fauna was part of a series of aquatic surveys of New York state conducted from 1926 through 1939 by the New York State Conserva-

tion Department, headed by E. Moore (Moore, 1930a). A limnological survey was conducted in 1960s and documented zooplankton and some benthic invertebrates (Henson and Potash, 1970). In the 1970s Myer and Gruending (1979) published a second limnological survey

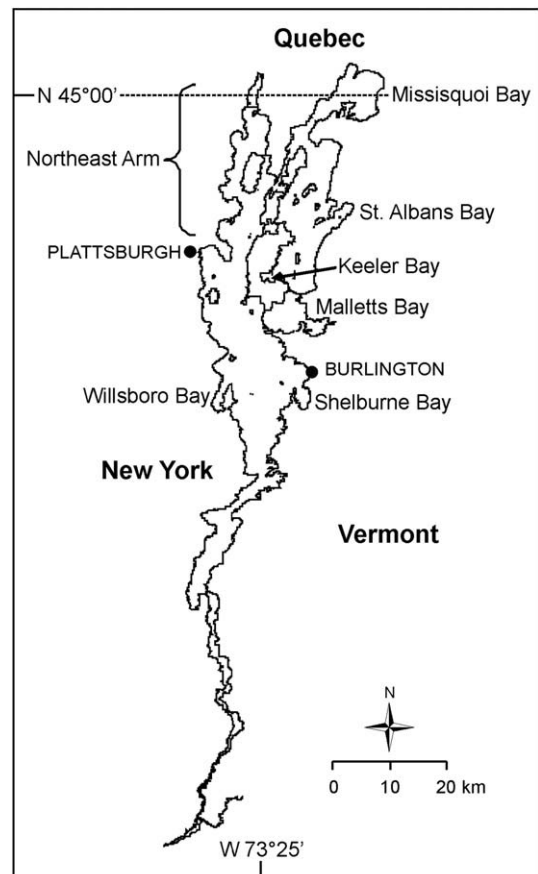


Fig. 1. Map of Lake Champlain, indicating sites mentioned in the text.

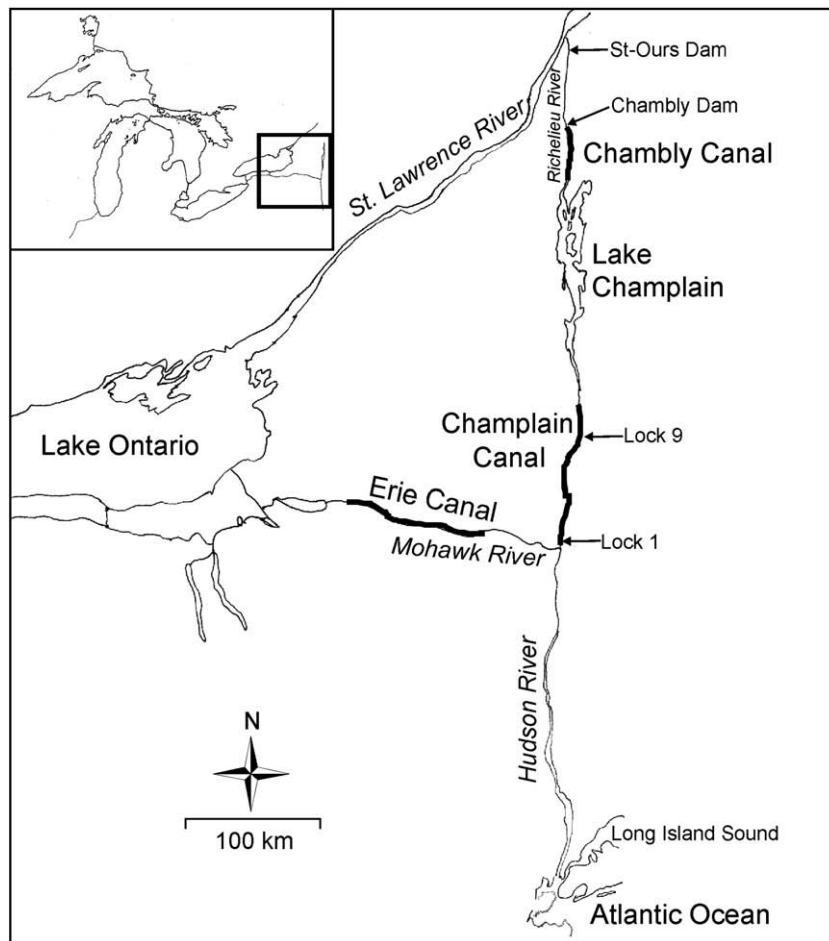


Fig. 2. Lake Champlain basin and connecting waterways, showing canals connecting historically separate watersheds through which exotic species may have gained access to the lake. Only the portion of the Erie Canal connecting the Lake Ontario and Mohawk River watersheds is highlighted. The Chambly Canal runs parallel to the Richelieu River, but does not create a new watershed connection.

of Lake Champlain which included data on the phytoplankton, zooplankton, and invertebrates of the lake. In the early 1950s a fish survey was conducted (Halnon, 1954). A survey of the macroinvertebrate fauna of rocky substrates was conducted in 1995, stimulated by the prospect of dramatic changes in the fauna due to the invasion of zebra mussels (Fiske and Levey, 1996).

The Vermont Department of Environmental Conservation (VTDEC) has sampled plankton annually since 1994 at 23 stations around the lake as part of a zebra mussel monitoring program (Kamman, 1994; Stickney, 1996; Eliopoulos and Stangel, 1999, 2001). Surveys of other fauna are often short-term, focused on small groups of taxa (e.g., salmonids, unionids), and tend to be dictated by funding for specific projects. Collections referred to in this paper are the invertebrate collections of the Biomonitoring and Aquatic Studies Section of the VTDEC, fish collections documented by Langdon et al. (2006), and collections by the Vermont Department of Fisheries and Wildlife (VTDFW) and New York State Department of Environmental Conservation (NYSDEC).

Results

A total of 46 exotic species are established (reproducing and self-sustaining) in the Lake Champlain basin, as indicated by broad geographic distribution, abundance, and sightings over several years. In addition, goldfish (*Carassius auratus*) have been sighted intermittently in the lake, but are not presumed to be self-sustaining. Goldfish are presumably reintroduced periodically via aquarium dumping. In contrast, for example, tench are caught periodically by

anglers throughout the northern portion of the lake, therefore the species is presumed to be reproducing in the lake. Black bullheads (*Ameiurus melas*) were collected prior to 1987 but have not been documented since then, so their status is unknown; we assume here that they are not self-sustaining. Of the 48 species in the basin, 44 are found in the lake proper or, in the case of emergent plants, along the shorelines of Lake Champlain. Bigwater crayfish (*Cambarus/Orconectes robustus*), freshwater jellyfish (*Craspedacusta sowerbyi*), and didymo (*Didymosphenia geminata*) are found only in the Lake Champlain basin but not in the lake proper, and rusty crayfish (*O. rusticus*) has so far only been found as close to the lake as the lower Winooski River.

Substantially more information is available for some of the more visible and high-impact species, especially plants and fishes, than obscure species such as planktonic organisms. Consequently, some of the species histories and documentation below are sparse; for more well-understood species, we have limited our discussion to information relevant to the route of invasion and potential impacts in the Lake Champlain basin.

Aquatic flora

Lythraceae

Purple loosestrife (*Lythrum salicaria*)

L. salicaria, a perennial wetland plant that spreads readily by seeds, was accidentally imported to North America from Europe and Asia on raw wool or sheep in the early 1800s (Thompson et al., 1987). Its

subsequent spread closely followed the development of canals and the waterborne commerce along those canals. By the turn of the 19th century *L. salicaria* was well established along the NY State Barge Canal (Thompson et al., 1987). It likely spread along the Champlain Canal into the Lake Champlain basin. Accidental releases from ornamental stocks may have also facilitated the plant's spread into the Lake Champlain basin. The 1929 biological survey of the Lake Champlain watershed noted that *L. salicaria* was locally common in marshes bordering Lake Champlain (Muenscher, 1930a). It has since been reported in more than 167 towns in Vermont (Copans and Garrity, 2003). An unknown, but significant amount of wetland area is infested within the Lake Champlain basin of New York and Quebec. Five thousand dollars were spent by the USFWS each year between 1986 and 1991 on chemical controls for purple loosestrife in the Missisquoi National Wildlife Refuge on the northeast end of Lake Champlain. An additional \$200,000 has been spent since 1996 in an ongoing effort to control purple loosestrife throughout Vermont with leaf-eating beetles (Alan Quackenbush, VTDEC, personal communication).

Haloragaceae

Eurasian water milfoil (*Myriophyllum spicatum*)

M. spicatum, a perennial, submersed aquatic plant native to Europe, Asia, and parts of Africa, is widely spread throughout North America (Countryman, 1978). The exact period of introduction to North America is not known, but likely occurred in the early 1900s. *M. spicatum* may have been intentionally introduced into the United States by the Plant Introduction Branch of the United States Department of Agriculture. The aquarium trade has also likely played a role in its initial introduction and spread.

The first discovery of *M. spicatum* in New England was made in St. Albans Bay, Lake Champlain in 1962. At that time *M. spicatum* was not found in southern portions of Lake Champlain (Countryman, 1975). A survey of Lake Champlain in 1976 showed that *M. spicatum* was present in all areas of the lake and it was estimated that several thousand acres of the lake were infested. It was also found to be the most abundant species present in a survey of eleven Lake Champlain wetlands (Countryman, 1978). *M. spicatum* continues to occupy an extensive range throughout the lake and it infests at least 40 other bodies of water throughout the Lake Champlain basin. New infestations of *M. spicatum* are discovered in Vermont nearly every year. Fragments attached to trailered boats are the likely cause of overland introductions.

M. spicatum can proliferate in high densities in lakes, and can cause serious impairments to boating, fishing and swimming. The plant's surface canopy and consequent reduction in light penetration can reduce or eliminate native aquatic vegetation as well as native fish and wildlife populations (Madsen et al., 1991). It has little value as food for waterfowl and through competition it can reduce the quantities of desirable duck food species (Aiken et al., 1979). At high densities it has been shown to support significantly fewer invertebrates than native plants (Keast, 1984). *M. spicatum* costs in Vermont since 1982 have exceeded \$4.1 million while the estimate cost of a three-year Eurasian watermilfoil control program initiated in 2004 on upper Saranac Lake, New York is \$1.5 million (Lake Champlain Basin Program, 2005).

Trapaceae

Water chestnut (*Trapa natans*)

T. natans, a native of Europe, Asia, and Africa was first discovered in North America in the 1870s in a small Massachusetts pond (Countryman, 1970). It was likely planted intentionally in Sander's Lake (now known as Collin's Lake), New York in 1886 (Wibbe, 1886; cited by Mills et al., 1993), from where it spread to the Mohawk River by 1920 and then downstream to the Hudson River. By 1952 water chestnut was estimated to infest 3500 acres in New York (Greeley,

1965). It was first documented in Lake Champlain in the early 1940s in shallow bays in the southern end on both the Vermont and New York shores. It is generally assumed that *T. natans* spread to Lake Champlain from the Mohawk or Hudson River and that this may have occurred by seeds hitchhiking on boats traveling through the Champlain Canal (Countryman, 1970).

T. natans displaces other aquatic plant species, is of little food value to wildlife, and forms dense mats which alter habitat and interfere with recreational activities (Hummel and Kiviak, 2004). Currently, extensive growth of *T. natans* in southern Lake Champlain severely restricts boat traffic and other recreational uses. Populations of water chestnut also exist in several inland lakes in the southern portion of Vermont. In 1998, the first population found in Quebec, Canada was located in the South River approximately 9 mi northwest of Missisquoi Bay, Lake Champlain (Bove et al., 2002). Plants have since been found in the Richelieu River and Pike River, Quebec (Hunt and Crawford, 2003). *T. natans* management on Lake Champlain between 1982 and 2004 has involved thousands of volunteer hours and more than \$5.8 million in state and federal funds.

Butomaceae

Flowering rush (*Butomus umbellatus*)

A perennial, aquatic plant native to Europe and Asia, *B. umbellatus* was first observed in North America in the St. Lawrence River near Montreal in 1897 (Anderson et al., 1974). Knowlton (1923) predicted that it would work its way up the St. Lawrence River and its tributaries into Lake Champlain. It was in fact discovered in the southern end of Lake Champlain in 1928 at Orwell, Vermont (Countryman, 1970). A 1929 survey indicated it was the dominant emerged plant in the southern part of Lake Champlain while it was not present in northern sections of the lake (Muenscher, 1930b). In 1929 *B. umbellatus* was well established along the entrance of the Champlain Canal at Whitehall, NY. One early reference suggested that the source of the Whitehall, New York population had been contaminated ballast dumped at Whitehall by ships from Montreal. The ballast was reported to consist of sand dug from St. Lawrence River banks where *B. umbellatus* was established (Burlington Free Press, 1937).

B. umbellatus reproduces by seed production and vegetative spread. Muskrats use *B. umbellatus* plant material for building their lodges and may facilitate its spread (Gaiser, 1949). It is now commonly found in marshes and along the shores of Lake Champlain and the St. Lawrence River. In southern Lake Champlain, dense stands appear to be crowding out native species in localized areas.

Hydrocharitaceae

European frog's bit (*Hydrocharis morsus-ranae*)

Hydrocharis morsus-ranae is an annual, primarily floating, plant native to Europe and Asia (Minshall, 1940). It is capable of producing dense mats of vegetation that limit light penetration and affect native plants. It can also negatively impact boating and recreational activities (Mehrhoff et al., 2003). It was first reported in the wild in North America in 1939 in the Rideau Canal at Ottawa, Ontario, Canada after escaping ornamental cultivation (Minshall, 1940). Dense mats of *H. morsus-ranae* readily tangle on the shaft of outboard boat motors and it was suggested that pleasure boat traffic would lead to the gradual spread of the plant through the locks of the Rideau Canal system (Lumsden and McLauhin, 1988). It also spread downstream in the Ottawa and St. Lawrence Rivers to near the mouth of the Richelieu River in Biertherville, Quebec leading Countryman (1978) to predict that *H. morsus-ranae* would spread to Lake Champlain on boats traveling through the Richelieu River and Chambly Canal. It was first recorded in the United States in 1974 in the Oswegatchie River in northern New York (Catling and Dore, 1982). A small population of *H. morsus-ranae* was discovered in northern Lake

Champlain near Grand Isle, Vermont in 1993 and in 1999 it was found in the southern end of Lake Champlain at Benson, Orwell, and West Haven, Vermont. In 2000 it was found in Mill Bay of Lake Champlain on the New York side of the lake. It is currently not at nuisance levels in Lake Champlain.

Iridaceae

Yellow flag iris (*Iris pseudacorus*)

I. pseudacorus, a wetland perennial plant native to Europe, the British Isles, North Africa and the Mediterranean region, with the potential to form dense monotypic stands and out-compete other plants (Sutherland, 1990). Although specific records of introduction in North America are sparse it is thought to have readily escaped from cultivation. It may spread downstream by broken rhizomes and possibly seeds (Sutherland, 1990). It has been used for erosion control and continues to be sold through garden and plant dealers. *I. pseudacorus* was brought to Canada as a garden ornamental and was reported growing in the wild in the early 1900s (Cody, 1961). In 1904 *I. pseudacorus* was observed in Burlington, Vermont, and was considered a “garden escape or waif coming from foreign seed” (Eggleston, 1904). *I. pseudacorus* has been observed in several locations around Lake Champlain, and in the Poultney River, Missisquoi River, and Lewis Creek, VT. It has also been observed in Lake Ellmore, VT within the Lake Champlain basin. While currently not at nuisance levels in the Lake Champlain Basin, it is reportedly a problem in other regions.

Poaceae

Common or giant reed (*Phragmites australis*)

P. australis is an aggressive herbaceous plant that can grow up to 15 ft in height. It spreads rapidly by underground rhizomes in disturbed wetland areas and can quickly dominate an area, displacing diverse native communities with a monoculture (Saltonstall, 2002). It is found in every state of the United States and there is evidence that the plant is native to the Northeast. However, recent genetic research has shown that an introduced European haplotype, likely introduced in the early part of the 19th century, has displaced native types in New England (Saltonstall, 2002). Although widely scattered throughout New York and Vermont, the extent of *P. australis* invasion has not been well documented.

Menyanthaceae

Yellow floating heart (*Nymphoides peltata*)

N. peltata is native to Europe and has been grown as a cultivated ornamental plant in water gardens in the United States since the late 1800s. It has spread rapidly since first reports of its escape from cultivation in New York State and is now established in at least 15 states. Muenscher (1935) reported dense beds of this plant in the Hudson River between Waterford and North Troy. It was first discovered in Lake Champlain in the 1950s (Countryman, 1978) and currently occurs only in limited areas of the southern part of Lake Champlain. The most extensive population in Lake Champlain occurs just north of Stony Point in Benson, Vermont. Countryman (1978) hypothesized that *N. peltata* entered the lake via the Champlain Barge Canal. *N. peltata* has the potential to shade and crowd out native aquatic plants and block waterways (Mehrhoff et al., 2003).

Potamogetonaceae

Curly leaf pondweed (*Potamogeton crispus*)

A submersed aquatic perennial native to Europe, Asia, Africa and Australia, *P. crispus* has spread aggressively since being introduced to North America in the mid-1800s. It is now established in all of the

continental United States except Maine and South Carolina (USDA-NRCS 2002). It has become invasive in many areas. In 1929 *P. crispus* was identified in Lake Champlain within submerged weed beds of Fields Bay and within Plattsburgh Harbor (Muenscher, 1930a). It has since been identified in at least 16 inland lakes within the Lake Champlain basin. It can form dense mats on the water surface that inhibit native aquatic plant growth and interfere with boating and other water recreation. It spreads primarily by vegetative turions (Mehrhoff et al., 2003).

Najadaceae

Slender-leaved naiad (*Najas minor*)

A submersed, annual aquatic plant native to Europe and Asia, *N. minor* was discovered in the Hudson River at Troy and Waterford, NY, at the mouth of the Mohawk River in 1934 (Clausen, 1936). It was thought to have been introduced there on shipping materials from Europe or possibly dumped from an aquarium. In 2002 several dense populations of *N. minor* were confirmed in several areas of southern Lake Champlain. Previously, it was observed in two Vermont lakes within the Lake Champlain basin. *N. minor* has the ability to form thick stands that can cover or clog a lake or stream. It can reproduce by seed but is primarily dispersed by fragmentation (Mehrhoff et al., 2003). Ducks may utilize the plant as a food source and likely facilitate its dispersal (Merilainen, 1968).

Brassicaceae

Great water cress (*Rorippa amphibia*)

R. amphibia is a perennial wetland plant native to Europe. It was reported from Auburn, Maine in 1928 (Norton, 1933), the St. Lawrence River near Montreal in 1929 (Marie-Victorin, 1964) and in Danbury, Connecticut in 1930 where it was thought to have been brought in on a nearby railroad or released from a nursery (Bradley, 1931). It is locally common near the mouth of the Missisquoi River in Swanton, Vermont, but otherwise does not appear to be at nuisance levels anywhere in the Lake Champlain basin.

Alismataceae

Water plantain (*Alisma gramineum*)

A perennial, aquatic plant native to Europe and western North America, *A. gramineum* was first reported in eastern North America around 1918 near Lonqueuil and Montreal, Quebec (Countryman, 1968). In 1948 it was reported as a “pesky weed” around Montreal that was progressively invading the Richelieu River valley (Raymond and Kucyniak, 1948). It was first reported in Lake Champlain in Shelburne Bay in 1961. At that time it appeared to be restricted primarily to the northern half of the lake. A subsequent survey in 1966 detected some *A. gramineum* in Addison County, Vermont, but none was found south of Panton, Vermont (Countryman, 1968). Countryman (1978) observed that during low water level *A. gramineum* may grow completely emerged and dominate the shoreline vegetation in Lake Champlain. The current status of this plant in Lake Champlain is unknown.

Bacillariophyceae

Didymo (*Didymosphenia geminata*)

Didymo, also known as rock snot, is a freshwater diatom native to northern Europe, Asia, and probably Canada (Spaulding and Elwell, 2007). The species was reported in the US, in Virginia, as early as 1975, and has since been found in several western states, New York, Maryland, and New Hampshire. In 2006, didymo was found in the Batten Kill River in Vermont. A colony was found in the Mad River in the Lake Champlain drainage in July, 2008 (Leslie Matthews, VTDEC).

Didymo forms thick carpets attached to stream substrates, smothering benthic fauna. The species can be readily transported on waders and recreational equipment.

Fishes

Salmonidae

Rainbow trout (*Oncorhynchus mykiss*)

Rainbow trout is native to the western United States, and has been stocked widely in the Great Lakes basin since 1876 (Emery, 1985). Rainbow trout were first stocked into Lake Champlain in 1972, and reproduced naturally in many streams in the basin. Stocking into streams throughout Vermont and New York is conducted annually to support a sport fishery (Fisheries Technical Committee, 2008).

Brown trout (*Salmo trutta*)

Brown trout, native to western Europe, is a popular sport fish, and has been deliberately introduced to locations throughout North America since 1883 (Fuller et al., 1999). Brown trout were first stocked into Lake Champlain in 1977, and continue to be stocked to support a sport fishery (Fisheries Technical Committee, 2008).

Cyprinidae

Goldfish (*Carassius auratus*)

The Asian goldfish has been present in North America since the late 1600s (DeKay, 1842), and has been introduced widely around the country by hatcheries, bait bucket releases, aquarium releases, and accidental escapes from hatcheries and ornamental ponds. Goldfish appear erratically in various portions of the drainage (Englesby Brook, Jewett Brook), likely as a result of aquarium releases, and are established in a few small ponds. Lake Champlain is likely too cold to sustain viable populations of this species.

Common carp (*Cyprinus carpio*)

The common carp, a native of Eurasia, was raised as a food fish in the United States by immigrant farmers as early as 1832 (Smith, 1985b). It was unintentionally released into the wild and is now found throughout much of the country. Carp are common throughout Lake Champlain; they were reported in collections prior to 1930, but not in a 1894 survey (Greeley, 1930; Evermann and Kendall, 1902). Greeley (1930) hypothesized that they entered the lake via the Champlain Canal. Carp are not highly abundant in the lake, and little is known about their impacts within the Lake Champlain basin.

European rudd (*S. erythrophthalmus*)

European rudd is a popular bait fish and is native to Eurasia. It was introduced into Columbia County, New York and became established there in 1936 (Smith, 1986). A population of European rudd was discovered in Keeler Bay, Lake Champlain in 1991 (C. McKenzie, VTDFW). They have also been reported in Burr Pond, Lake Bomoseen, Lake Hortonia, and Roach Pond in Vermont, all within the Lake Champlain basin. The status of these populations is currently unknown. Their appearance in Lake Champlain may be from a bait bucket introduction.

Tench (*T. tinca*)

Tench is native to Europe and parts of western Asia, and was introduced into the US in the 1877 for food and sport (Fuller et al., 1999). Tench has been documented in 38 states (Fuller et al., 1999). Tench were imported illegally for use in fish culture in Quebec in 1986, and escaped from fish farm ponds in 1991 (Vachon and Dumont, 2000). Commercial fishermen found tench in the Richelieu River in 1994, (Vachon and Dumont, 2000). A single individual (45 cm TL) was caught in the Great Chazy River in late May 2002 (unpubl. obs.), and a second individual was caught there in 2005 (VTDFW, unpub. data).

Tench have been reported intermittently by anglers in the northern portions of the lake since 2002 (Brian Chipman, VTFW). Population size and impacts are currently unknown.

Clupeidae

Gizzard shad (*D. cepedianum*)

Gizzard shad, a plankton-eating fish native to the Atlantic Coast drainages from New York to Florida, and the Great Lakes, has naturally expanded its range into the Connecticut River. Gizzard shad was first sighted in southern Lake Champlain, below Benson's Landing, in 1993, having probably entered via the Champlain Canal (Chet MacKenzie, VTDFW). It is not known to be in any other bodies of water in Vermont. Currently, there are no plans to manage the gizzard shad population in Lake Champlain.

Blueback herring (*A. aestivalis*)

The blueback herring is native to the Hudson River and the lower Connecticut River in Connecticut and Massachusetts, but is not considered a native of the Lake Champlain basin. This anadromous fish has expanded its range in New York through the canal system. It was first reported in Lake Champlain on the New York side in the late 1970s and on the Vermont side in 1997 (VTDFW). It likely migrated into the lake from the Hudson River through the Champlain Canal; entry from the north is unlikely, as blueback herring are not present in the Gulf of St. Lawrence (Smith, 1985b). Blueback herring are believed to have the potential to displace smelt and other native forage fish.

Alewife (*A. pseudoharengus*)

Alewife is an anadromous fish that is native to the Atlantic Ocean. The species invaded the Great Lakes via the Welland Canal in 1931, and caused dramatic declines in native planktivore populations (Smith, 1970). Alewife was introduced into Green Pond in Franklin County, NY, within the Lake Champlain watershed, in 1957, and was seen in the late 1970s and early 1980s in the Richelieu and Pike rivers (Good and Cargelli, 2001). A large population of alewives was discovered in Lake St. Catherine in Poultney, Vermont in 1997. Fisheries biologists with the VTDFW suspect that the alewife was intentionally introduced to Lake St. Catherine by anglers hoping to increase the numbers of forage fish available to sport fishes. Seven alewives were found in Missisquoi Bay in 2003 (Bernie Pientka, VTDFW), and the population expanded dramatically in 2007; large numbers of young-of-year alewife were collected in gillnets, and a substantial die-off occurred in the southern lake in spring, 2008.

Atherinidae

Brook silverside (*Labidesthes sicculus*)

Brook silverside is native to the St. Lawrence and Richelieu Rivers in Quebec, and the Allegheny and St. Lawrence River drainages. The species expanded its range, probably via the canal system, to the Mohawk River in the 1930s, Oneida Lake in New York in 1983, and to the Hudson River in 1991; however, Mills et al. (1996) do not list this species as nonindigenous in the Hudson River. Brook silverside was found in four of the five basins of Lake Champlain, from Alburg to the Poultney river, in 1998 (Marsden et al., 2000). The route of introduction of brook silverside is unclear; they could have entered the lake from the Mohawk River via the Champlain Canal at the south end or from the Richelieu River via the Chambly Canal at the north end. The potential impact of brook silversides in the lake is not known.

Ictaluridae

Black bullhead (*A. melas*)

Black bullhead is widespread in North America, but in New York the species has only been found in the western part of the state (Smith, 1985b). This species appeared in the Lake Champlain basin in

surveys prior to 1987 (Carlson and Daniels, 2004) and were likely introduced for angling.

Centrarchidae

Largemouth bass (*Micropterus salmoides*)

Largemouth bass is widely distributed throughout North America, including the Great Lakes and Mississippi River system. The species has been widely stocked as a sport fish. It was apparently absent from eastern New York and Vermont until it spread to the Mohawk–Hudson drainage via the Erie Canal, and was stocked in New England around 1950 (Smith, 1985b; Carlson and Daniels, 2004).

Black crappie (*Pomoxis nigromaculatus*)

This species is native to the St. Lawrence watershed and throughout several western states, Quebec, and Manitoba (Smith, 1985b). It was recorded in the lake by 1930 (Greeley, 1930; Carlson and Daniels, 2004) and may have been deliberately introduced as a sport fish.

White crappie (*Pomoxis annularis*)

White crappie is native to western New York state (Langdon et al., 2006). White crappie are currently found only in the south lake and its tributaries, and are uncommon (Langdon et al., 2006), though they were very abundant in the area south of Benson's Landing in 1993–94 (Donna Parrish, University of Vermont).

Moronidae

White perch (*Morone americana*)

White perch, a marine invader, has been present in the lake since 1984, and is believed to have entered the lake via the Champlain Canal (Hawes and Parrish, 2003). It had been present in the Hudson River for many years prior, but prior to improvements in water quality, the high levels of pollution in the river near the mouth of the canal may have acted as a barrier to the fish's spread. The white perch is now common in most of Lake Champlain.

Molluscs

Bithyniidae

Faucet snail, mud bithynia (*Bithynia tentaculata*)

The mud bithynia or faucet snail was introduced from Europe to the Great Lakes in the ballast of timber ships. The snails were found abundantly in the Champlain Canal in 1879, from where they likely spread to Lake Champlain. The species has been found in Lake Champlain at multiple sites north of Burlington (Fiske and Levey, 1996; Brown et al., 1993), and a riverine wetland along the Winooski River. It is probable that the species is more widespread than currently documented. They were found in abundance at the Grand Isle ferry dock in 1997 (Eliopoulos and Stangel, 1999). The snail competes with native snails of the family Pleuroceridae. At locations where the mud bithynia has been observed in Lake Champlain, it generally dominates the snail fauna (Fiske and Levey, 1996).

Lymnaeidae

Big-ear radix, European ear snail (*R. auricularia*)

Big-ear radix is a Eurasian species that was found in the Hudson River near Troy, NY prior to 1869 (Strayer, 1987). Their appearance at several locations around the Great Lakes appears to be linked to transportation on ornamental plants (Mills et al., 1993). This snail was found in Vermont in 1944 in the Walloomsac River near Shaftsbury (Johnson, 1945), and was first noted in Lake Champlain at the Grand Isle ferry dock in October 1999 during biological sampling (P. Stangel, VTDEC).

Woodland pondsnail (*S. catascopium*)

This species, also listed as *Lymnaea catascopium*, is native to western New England and the lower four Great Lakes, and was reported in western New York by De Kay (1843). In the mid- to late 1800s it was reported in the Erie Canal (Jokinen, 1992). The woodland pondsnail has been collected from several locations in northern Lake Champlain since 1994 (Steve Fiske, VTDEC). Similar to *Pleurocera acuta* (below), this species is fairly widespread; its classification here as exotic to Lake Champlain is based on the extensive review by Jokinen (1992) in which it did not appear in the basin. The species is an intermediate host for the schistosome parasite that causes swimmer's itch (present in Lake Champlain); however, other snails that are native to Lake Champlain are also potential hosts.

Hydrobiidae

Buffalo pebblesnail (*Gillia altilis*)

This species is native to the Atlantic coastal drainage, and apparently entered the Great Lakes from the Hudson River drainage via the Erie Canal in the early 1900s (Mills et al. 1993). It may have invaded Lake Champlain via the Champlain Canal connection to the Erie Canal. It was noted in several locations from North Hero to the Poultney River in VTDEC collections dating from 1993.

Pleuroceridae

Sharp hornsnail (*Pleurocera acuta*)

This species was found in early surveys in several sites throughout New York (De Kay, 1843; Jokinen, 1992); however, it is believed to have migrated to the Hudson River basin via the Erie Canal (Smith, 1983; Strayer, 1987), and therefore may have been introduced to Lake Champlain by the same route, using the Champlain Canal.

Viviparidae

Chinese mystery snail, Oriental mystery snail (*Bellamya (Cipangopaludina) chinensis*)

The Chinese mystery snail was introduced from Asia into the Chinese markets of San Francisco as a food item in the late 1800s. It has spread across the United States and where it occurs it is locally abundant (Smith, 2000). It was first observed in New York Niskayuna (Mohawk River basin) in 1920 (Strayer, 1987) and was probably introduced into Vermont in the 1960–70s, possibly to help control algae in small private ponds. It was found in the Lake Hortonia outlet of the Hubbardton River, in the Lake Champlain basin in 2003 (Steve Fiske, VTDEC).

Banded mystery snail (*Viviparus georgianus*)

The banded mystery snail is native to the Mississippi drainage and the southeast. A population of 200 individuals was transported from Illinois and deliberately introduced into the Erie Canal in Herkimer Co. in 1867 (Mills et al., 1993). This species is present in several inland lakes in the Champlain drainage, at Isle La Motte, Province Point, Savage Point, and Ladd Point in Lake Champlain. VTDEC collections in the drainage date from 1988.

Valvatidae

European stream valvata, European valve snail (*Valvata piscinalis*)

This European species was likely transported to North America in packing material used in shipping; it appeared in Lake Ontario in 1897 (Baker, 1989 cited in Mills et al., 1993), and has spread through the lower Great Lakes. Pagel (1969) found it to be the

dominant species in Malletts Bay and St. Albans Bay in the 1960s, but in the early 1970s it was replaced in St. Albans Bay by *Valvata tricarinata* (Myer and Gruendling, 1979).

Dreissenidae

Zebra mussel (D. polymorpha)

The zebra mussel, a small freshwater mollusc native to eastern Europe, was first found in Lake St. Clair in 1988 and is presumed to be a ballast water introduction. The zebra mussel was first discovered in the southern end of Lake Champlain in 1993; an adult mussel was found and identified by a boy who had seen a Zebra Mussel Watch Card (Matthew Toomey, pers. comm.; Soper, 1993). The mussels likely entered Lake Champlain through the Champlain Canal, as they expanded into the lake from south to north, and are still scarce in the northeastern portions of the lake (Eliopoulos and Stangel, 2001; unpubl. data). The Richelieu River is also infested with zebra mussels, likely a result of range expansion from Lake Champlain or the St. Lawrence River. They densely cover all hard substrates in the southern half of the lake, and began densely colonizing soft substrates in the 2000s (Beekey et al., 2004).

Sphaeriidae

European fingernail clam (Sphaerium corneum)

This species is native to Eurasia, but is now present in the lower Great Lakes and the St. Lawrence River (Mills et al., 1993). The date of arrival of this species in Lake Champlain is unknown, though Burch (1972) noted that it was present in Lake Champlain and Lake Erie. The species was present in VTDEC collections in several locations in the northern lake as of 1995.

Greater European pea clam (Pisidium amnicum)

This species was known in Lake Ontario as early as 1897 (Baker, 1898; cited in Mills et al., 1993), and is present in the lower Great Lakes and St. Lawrence River. Burch (1972) reported it from Lake Champlain. Its vector of introduction is unknown.

Crustaceans

Cambaridae

Rusty crayfish (O. rusticus)

Rusty crayfish, native to the Ohio River Basin, have spread to many northern states causing negative ecological impacts (Olsen et al., 1991). It was likely transported to these new areas as fishing bait. Rusty crayfish have been reported in Lake Carmi in Franklin, Vermont, and in the lower Winooski River (VTDEC). It is also found in the Connecticut and White rivers (VTDEC). This aggressive crayfish may out-compete native crayfish as it has a high metabolic rate and consequently consumes more food than native crayfish.

Allegheny crayfish (Orconectes obscurus)

As of 1971 this species was found only from the town of Hartland on the Connecticut River; Bell (1971) felt that this population was introduced by fishermen. It was found in Isle La Motte and Province Point in Lake Champlain in 1993 and 1995, but its date of introduction to the lake is unknown (VTDEC).

Bigwater crayfish, robust crayfish (Cambarus/Orconectes robustus)

This species is not native in New England (Bell, 1971); it was found in the upper Saranac River, NY, by Crocker (1957), and a single potentially questionable specimen was found in Pond Brook, VT in 2002 (Steve Fiske, VTDEC).

Bosminidae

Water flea (Eubosmina coregoni)

E. coregoni is a European species that was first found in the Great Lakes, in Lake Michigan, in 1966 (Wells, 1977, cited by Mills et al., 1993). It is presumed to have entered the lakes in ballast water, and has since spread to all of the lakes. *E. coregoni* was found throughout Lake Champlain in surveys in 1991 (Brown et al., 1992).

Cyclopidae

Cyclopoid copepod (Thermocyclops crassus)

This species is native to Eurasia and Africa; its discovery during surveys in 1991 represents the first record in North America (Duchovny et al., 1992). It was found mostly in Missisquoi Bay.

Other invertebrates

Coelenterata

Freshwater jellyfish (Craspedacusta sowerbyi)

This species of freshwater jellyfish is native to the Yangtze River in China, and was spread to Europe and the United States with the use of ornamental aquatic plants. It was first recorded in the US in 1880, and is now present in at least 44 states (<http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=1068>). *C. sowerbyi* appeared in Lake Erie in 1934, presumed to be an aquarium release. *C. sowerbyi* is also present in the Hudson River, and so has access to Lake Champlain via the Champlain Canal. It was first recorded in the Champlain drainage in Greenwood Lake, Woodbury, VT in 1995, and has been reported in several ponds in Vermont and New York since then (M. Ferguson, VTDEC).

Turbellaria

Vortex worm (Dugesia lugubris/Schmidtea polychroa)

This species is native to Europe. Its first confirmed identification in North America was by Ball (1969), who collected specimens from the St. Lawrence River, northeastern Lake Ontario, and Lake Champlain at the Burlington ferry dock in 1968. Ball hypothesized that this flatworm made its way into Lake Champlain assisted by shipping in the Richelieu River, which would likely have involved the Chambly Canal. The species appears to be synonymous with *D. polychroa*, which has recently been renamed *Schmidtea polychroa*.

Pathogens

Muskellunge and northern pike lymphosarcoma

This viral disease, known only from northern pike (*Esox lucius*) and muskellunge (*Esox masquinongy*), is a malignant blood cancer that is detected by the presence of skin lesions (Sonstegard and Hnath, 1978). Survival of infected fishes is less than 1%. The disease is known in North America throughout Ontario and in New York and Michigan; it is readily transmitted through stocked fish (Sonstegard and Hnath, 1978). It was first seen in Lake Champlain in 2002, and appeared in 20% of muskellunge and northern pike taken from the northern portion of the lake (Tom Jones, VTDFW). It is possible that the virus was present but undetected prior to 2002.

Largemouth bass virus

This virus was found in surveys of bass in Lake Champlain in 2002; previously, there had been no reports of clinical signs or

death due to the disease, indicating that it was absent from the lake. The virus is present in southern states, Michigan, and Indiana, and caused a die-off in 1995 in South Carolina.

Species of debated status

Several additional species have been listed by one or more authors as exotic to Lake Champlain, but other authors contend they are native; therefore, we conclude that their status as exotics is in debate. Other species, such as the crayfish *Orconectes limosus*, the amphipod *Gammarus fasciatus*, and the polychaete worm *Manayunkia speciosa* may be either too obscure, or too difficult to discriminate from the native species, for historic work on their distribution to have clearly described their historic range.

Fishes

Petromyzontidae

Sea lamprey (P. marinus)

Recent genetic work suggests that sea lamprey is native to both Lake Ontario (Waldman et al., 2004) and Lake Champlain (Bryan et al., 2005). However, the absence of any historical reference, either in scientific literature or popular media, to sea lamprey or wounding on fishes is puzzling. Attacks by adult sea lamprey on salmon, lake trout, and other fish species have limited the full development of a Lake Champlain fishery, and restricted recreational and associated economic opportunities. Annual costs to control populations of sea lamprey in Lake Champlain are approximately \$340,000. The supposed exotic status of sea lamprey provided additional justification for the control program; however, it continues to warrant control as a nuisance species.

Osmeridae

Rainbow smelt (O. mordax)

Rainbow smelt is non-native in other portions of the Saint Lawrence drainage (Bailey and Smith, 1981), but is generally presumed to be native to Lake Champlain. Observations of smelt in the lake date from 1842 (Greene, 1930), although Thompson (1853) stated that smelt “occasionally makes his appearance” in Lake Champlain. Mandrak and Crossman (1992) and Bernatchez (1997) contend that smelt were present in the Champlain Sea, supported by fossil evidence. The status of smelt is complicated by the presence of two ‘races’ of smelt in the lake, a normal and a giant form (Zilliox and Youngs, 1958); Greene (1930) suggested that these may reflect the presence of descendants of both native and stocked anadromous smelt, as over 58 million smelt were stocked from the Cold Spring Harbor hatchery between 1919 and 1928. The genetic work of Bernatchez (1997) revealed only a single mtDNA haplotype in the lake, suggesting an origin from the Atlantic via the Hudson River valley; however, he may not have sampled the giant ‘race’.

Esocidae

Redfin pickerel (Esox americanus americanus)

This species is native to the Hudson River drainage, and is listed as exotic to Lake Champlain by Underhill (1986) and Carlson and Daniels (2004), despite its appearance in collections since the 1930s. Scott and Crossman (1973) felt that it was an invader in Canada via the Champlain Canal. However, specimens of redfin pickerel in various collections from the Castleton drainage support its status as a native (Langdon et al., 2006)

Molluscs

Hydrobiidae

Globe siltsnail (Birgella subglobosa)

The globe siltsnail is found in the Hudson River drainage and throughout the Great Lakes (Thompson, 1984; Jokinen, 1992); it is believed to have been introduced into the Erie Canal at Mohawk after 1860 and is present in Lake Champlain (Jokinen, 1992), but its status as a native or exotic in Lake Champlain is unknown.

Sphaeriidae

Henslow peaclam (Pisidium henslowanum)

This species, native to Europe, was previously suggested to be an exotic in the Great Lakes (Burch, 1972), but has been re-identified as native to North America (Smith, 1986). This species is present in Lake Champlain.

Unionidae

Elktoe (Alasmidonta marginata)

The elktoe mussel is present in the Hudson River, and was found for the first time in the Lake Champlain drainage in the Lamoille River in 2000 (Mark Ferguson, VTDFW). There is no compelling reason to suppose this species, which normally has an erratic and sparse distribution, is not native to the drainage. Few river surveys for unionids have been conducted that adequately surveyed the rocky substrates preferred by this species.

Other invertebrates

Cambaridae

Virile crayfish (Orconectes virilis), and calico crayfish (Orconectes immunitis)

Both of these species are native to North America, and have been spread as bait for sport fish. While listed as exotic to the Champlain basin by Benson (1999), Taylor et al. (2007) list both species as native to New York but potentially exotic in Vermont. The species are widely dispersed and there is no strong evidence to indicate that they are not native to the area; Bell (1971) lists them as native.

Crayfish (O. limosus)

Bell (1971) stated that the status of this species is uncertain; if exotic, it would have entered the Lake Champlain basin via the Champlain Canal or in bait buckets. Taylor et al. (2007) list this species as native to New York, but not present in Vermont.

Amphipoda

Gammarid amphipod (G. fasciatus)

G. fasciatus is present in the Hudson, Delaware, St. Lawrence, and Chesapeake drainages, and may be a non-native introduction in the Great Lakes (Mills et al., 1993). This species was abundant in Lake Champlain in 1975, but did not appear in collections in 1991 (Brown et al., 1992). Its status as a native or non-native in Lake Champlain is unknown.

Sabellidae

Polychaete worm (M. speciosa)

This species was found in Burlington Harbor mud in the late 1960s by Henson and Potash (1970), who stated that it was the first record in New England for the species and hypothesized that it may have been introduced via commercial shipping. The species is native

to North America, and has been found in Lakes Erie and Ontario. It is small and obscure, and its presence is often missed or not reported in samples (Mackie and Quadri, 1971), so there is no compelling reason to suppose that it is not native to New England and Lake Champlain.

Discussion

Compared with the Great Lakes, St. Lawrence River, and Hudson River, the Lake Champlain basin has received few invasions; 46 species have become established in the basin and 2 species have appeared intermittently, compared with >180 in the Great Lakes, 87 in the St. Lawrence River, and 113 in the Hudson River (de Lafontaine and Costan, 2002; Ricciardi, 2006; Strayer, 2006). This is an underestimate, as it does not include a thorough review of planktonic or many benthic invertebrate species (see above); however, we can be reasonably certain that many of the invaders in these taxa in the other watersheds (e.g., water flea *Daphnia lumholtzi*, spiny water flea *Bythotrephes longimanus*, quagga mussel *Dreissena bugensis*) are currently absent from Lake Champlain.

The relative paucity of exotic species in Lake Champlain is largely attributable to the absence of modern commercial traffic in the lake. While barges and smaller commercial vessels do enter the lake through the Champlain Canal, no vessels containing ballast water from outside North America have access to the lake because of the restricted size of the waterways into the lake. Mills et al. (1996) estimated that shipping was responsible for 33% of the invasions into the Great Lakes, and 13% of invasions into the Hudson River; de Lafontaine and Costan (2002) estimated that shipping had introduced 40% of the exotic species in the St. Lawrence River and Great Lakes. The only exotic species believed to have entered the Lake Champlain basin due to shipping is flowering rush (*B. umbellatus*), which apparently arrived in solid ballast from Montreal in the early 1900s (Burlington Free Press, 1937).

The major vector for exotic species introductions into Lake Champlain has been canals; 60% of the 26 invaders in the basin for which invasion routes can be guessed at entered the lake via the Champlain or Chambly canals (Table 1, Fig. 3). The remaining species were deliberately stocked (rainbow trout, brown trout), accidentally released from culture (goldfish, tench, big-ear radix), released from bait buckets (rudd, rusty crayfish), were transported on recreational equipment (didymo), or were deliberate but unauthorized releases (alewife, purple loosestrife *L. salicaria*). The propensity of managers and fishermen to move fishes into local

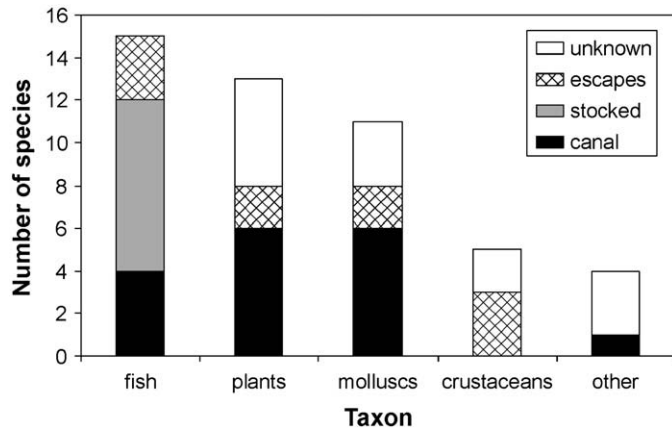


Fig. 3. Taxonomic groups of species introduced into the Lake Champlain basin, with vectors of introduction. Deliberate and unauthorized introductions are included under 'stocked', bait bucket releases, escapes from horticulture, and accidental transport are included under 'escapes'.

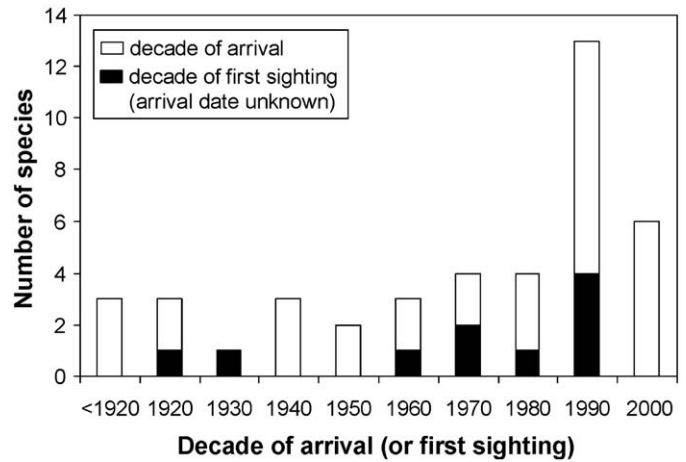


Fig. 4. Timeline of exotic species arrivals into the Lake Champlain basin, by decade. Species whose arrival date is unknown are shown in the decade in which they were first sighted, in the filled portion of each bar.

bodies of water, either as sport fish or as forage for sport fish, has led to considerable rearrangement of taxa; this creates a challenge for identifying origins of some fish species such as largemouth bass (*M. salmoides*) and crappies (*Pomoxis* spp.). We have not included species which were introduced historically by fishery managers but never became established; these include sockeye salmon (*Oncor-*), American shad (*Alosa sapidissima*), splake (*S. namaycush* × *fontinalis* hybrids), and tiger muskellunge (*E. lucius* × *E. masquinongy*) (Halnon, 1963; Carlson and Daniels, 2004).

The exotic species in the Lake Champlain basin are dominated by fishes (15), plants (13), and molluscs (11), plus five crustaceans and four other species (Table 1, Fig. 3). The large number of fish species has already been explained; plants have also been the focus of deliberate plantings as well as canal transport, though the vector for many of them is unknown. Molluscs are not generally a target for stocking (except big-ear radix), and are not highly vagile. Snails may make their way slowly through the canals, and mussel glochidia may be transported on their fish hosts, but the long-distance movement of fingernail clams required for invasion is difficult to explain, unless they can be transported by waterfowl.

Similar to the Great Lakes, the rate of introductions of exotic species into the Lake Champlain basin has increased dramatically in recent decades; 35% (17) of the introductions occurred between 1990 and 2000 (Fig. 4). Some of this increase is likely a consequence of improved water quality in the canals, as ten of the 23 introductions detected in the last three decades likely entered the lake via the canals. Prior to the 1960s, water quality in the canals was extremely poor and oxygen levels were likely too low to support a diversity of aquatic animal life (Daniels, 2001). An additional two species, rainbow trout and brown trout, were deliberately introduced to supplement the harvest for the growing sport fishing industry around the lake. However, some species may have been in the lake for some time and were only noticed recently as a consequence of increased sampling and research activity; for example, *E. coregoni* and *T. crassus*, reported in the 1990s, are tiny and obscure.

The majority ($N=25$, 52%) of exotic species in Lake Champlain are native to Eurasia; 10 are native to New England and the Atlantic drainage, and the remainder originated from elsewhere in the United States. The Eurasian species all reached the lake indirectly, having arrived in other parts of North America and subsequently spread by secondary vectors to Lake Champlain.

Impacts of exotic species in Lake Champlain

While the ecological or economic impact of many exotic species is negligible or difficult to detect, five species in particular have caused significant problems in Lake Champlain. Water chestnut, Eurasian watermilfoil, and purple loosestrife have crowded out native plant species, reduced habitat value for native animals, and reduced recreational access to the lake for swimmers and boaters. Water chestnut control cost \$5.8 million from 1982 to 2004, and annual removal and management costs nearly \$500,000 (Hunt and Marangelo, 2005). Zebra mussels have clogged water intakes, reduced recreational value of beaches and swimming areas, eliminated or severely reduced native mussel populations, and necessitated a \$1.6 million retrofitting of water intake lines to a state hatchery (K. Kelsey, VTDFW, pers. comm.). Approximately \$1 million was spent in monitoring and cleaning zebra mussels from municipal and industrial facilities through 2002, and an additional \$65,000 is spent annually in management of this species. An alewife die-off occurred in the spring of 2008, resulting in windrows of dead and dying fish throughout much of the southern third of the lake; 50–60 tons of alewife were removed from Port Henry alone. The invasion of alewife is fairly recent (2003), so these impacts are likely to increase in extent and severity; reproduction of native fishes that consume alewife is likely to be impacted by thiaminase, as has been seen elsewhere in the Great Lakes (Fitzsimons et al., 1999).

Effects of other species traditionally labeled as nuisances have not been readily apparent in Lake Champlain. Common carp tend to destroy macrophyte beds and increase local water turbidity as they forage in soft sediments; these behaviors have not been reported to cause problems in the lake. White perch (*M. americana*) are a concern because they can compete with yellow perch (*Perca flavescens*) and they consume fish eggs (Schaeffer and Margraf, 1987), but as yet no significant effect of their introduction has been noted in Lake Champlain (Hawes and Parrish, 2003). *Esox lymphosarcoma* was noted for the first time in Lake Champlain in 2002 and affected 20% of the northern pike and muskellunge in the northern section of the lake; the long-term effect of this pathogen on population health of these species and fishing interests has yet to be realized.

Effects of other exotics are more obscure. Rusty crayfish displace native crayfish and may damage macrophyte beds (Olsen et al., 1991), but their populations in the Lake Champlain basin are still small, and the species has not been a focus of research in the lake. The faucet snail (*B. tentaculata*) is reputed to compete with native pleurocerid snails, and it dominates the benthic fauna in areas where it is found (Harman, 1968). Woodland pondsnails are alternate hosts for the parasite that causes swimmer's itch; however, there are native species that also are hosts for the parasite, and it is unclear whether the addition of another host has altered the epidemiology of the parasite in Lake Champlain. It is critical to keep in mind that most of the exotic species in Lake Champlain have not been well studied, if at all. Impacts of species such as the common reed and faucet snail likely occurred decades ago, so comparisons with pre-invasion conditions cannot now be made. Other species, such as blueback herring, have invaded too recently for effects to be seen. In addition, effects of some species such as white perch may be masked by concurrent changes in the watershed due to other anthropogenic influences. Eutrophication, a consequence of phosphorous and nitrogen inputs from surrounding farmland, has resulted in noxious blooms of blue-green algae in Missisquoi Bay and St. Albans Bay. Zebra mussels, which can contribute to blue-green algae blooms, are rare in these two areas, but white perch consumption of zooplankton grazers could contribute to the problem (Couture and Watzin, 2008).

Lake Champlain as a vector for exotic species transfer

The problem of exotic species in Lake Champlain extends significantly beyond the boundaries of the lake. Lake Champlain lies at a crucial intersection between three major drainage systems, the Great Lakes, St. Lawrence River, and Hudson/Mohawk rivers (Fig. 2). In consequence, any species entering Lake Champlain has access to each of these systems via the canals or the Richelieu River. Historically, habitat conditions in these canals may not have been conducive to fish movement (Daniels, 2001). Some of the exotics in southern Lake Champlain are still absent from the Hudson River, including giant water cress, black bullhead, and the flatworm *Dugesia polychroa*. In recent decades, however, water quality in the canals has improved, increasing the likelihood that organisms could successfully traverse the canal or be carried through the canals by boats. For example, various authors have attributed the presence of silver lamprey (*Ichthyomyzon unicuspis*) and bowfin (*Amia calva*) in the Hudson River to passage through the Champlain Canal (Mills et al., 1999). Recent sampling at locks 8 and 9, the high point between the Hudson and Champlain drainages, revealed adults and juveniles of two mussel species not present in the Hudson River, fragile papershell (*Leptodea fragilis*) and pink heelsplitter (*Potamilus alatus*); both are native to Lake Champlain and were found on the Hudson River side of lock 8 (unpublished data). The possible use of Lake Champlain as an exotic species 'highway' highlights the need for biological barriers on the two canals linking Lake Champlain to the Great Lakes, Hudson and St. Lawrence rivers: these canals not only leave Lake Champlain vulnerable to future invasions, but represent a threat to the other systems as well.

Future invasion potential into Lake Champlain

The increase in arrivals of exotic species in Lake Champlain in the last two decades indicates that the invasive species problem is continuing, if not worsening (Fig. 4). Numerous aquatic or wetland species are present in nearby waters or are sold through nurseries, aquarium stores, or bait shops within or near the Lake Champlain basin. Nearby species include fanwort (*Cabomba caroliniana*), which has spread to New York, Massachusetts, Connecticut, and New Hampshire (Countryman, 1978), and the South American species Brazilian elodea (*Egeria densa*) and parrot's feather (*Myriophyllum aquaticum*), both found in New York (Weldy and Werier, 2005; ERDC). Northern snakehead (*Channa argus*), a predatory fish that has appeared in California, Florida, Maryland, New York, and Wisconsin within the last 6 years, may continue to spread as a result of aquarium dumping and the importation of live fish for Asian markets. Several species that have the potential to be ecologically or economically harmful are spreading rapidly through other parts of the Great Lakes or eastern North America.

Of particular concern are species that are in bodies of water connected to Lake Champlain via the canals. Fish-hook flea (*Cercopagis pengoi*) was discovered in Lake Ontario in 1998 (MacIsaac et al., 1999) and has since spread to Lake Michigan, Lake Erie, and the Finger Lakes of New York. The New Zealand mud snail (*Potamopyrgus antipodarum*) was found in Lake Ontario in 1991, and has since spread to Lake Erie (Levri et al., 2007; Zaranko et al., 1997). *D. lumholtzi*, *Echinogammarus ischnus*, calanoid copepods *Eurytemora affinis* and *Skistodiaptomus pallidus*, and a bacterium (*Thiopicla ingrica*) are in Lake Ontario (Faber and Jermolajev, 1966; Witt et al., 1997; Benson, 1999; Muzinic, 2000; Makarewicz et al., 2001; Dermott and Legner, 2002). White river crayfish (*Procambarus acutus acutus*), *Orconectes neglectus*, a gammarid amphipod (*Gammarus daiberi*), an oligochaete (*Ripistes parasita*), the European fouling hydroid (*Cordylophora caspia*), grass carp (*Ctenopharyngodon idella*), and bitterling (*Rhodeus sericeus*), among others, are in the Hudson River (Daniels et al., 2001; Simpson and Abele, 1984; Mills et al., 1996). The Asian bryozoan *Lophopodella carteri* is present in the Great Lakes and St. Lawrence River (Ricciardi and Reisinger, 1994; Rogick, 1934), and the round goby

(*Apollonia (Neogobius) melanostomus*), an aggressive fish known to displace native benthic fishes such mottled sculpin (*Cottus bairdi*) and darters (Janssen and Jude, 2001), is now in eastern Lake Ontario, the St. Lawrence River near Quebec City, and Lake St. Francois near Massena, New York (de Lafontaine and Costan, 2002). Either of these species could therefore enter Lake Champlain via either the Champlain or Chambly canals. Some species, such as the quagga mussel and Piedmont elimia snail (*Elimia (Goniobasis) virginica*), have already extended their range into the Erie Canal. The spiny water flea *B. longimanus* is established in Sacandaga Lake that drains through the Glen Falls Feeder Canal directly into the Champlain Canal at the midpoint between the Hudson and Champlain drainages (NYSDEC), thus the only obstacle to their entrance into Lake Champlain is a single lock. The problem of the canal connection is highlighted by the recent finding of the Asian clam, *Corbicula fluminea*, just below lock 8 in the Champlain Canal in April, 2007; this places the species two locks away from the Lake Champlain side of the canal (Kathleen Presti and Denise Mayer, New York State Museum, pers. comm.). Previously, *C. fluminea* was found in the Erie Canal near Lockport, NY, in 1998 (USFWS, 2003). Of greater concern is the possible role of canals in transmission of viral hemorrhagic septicemia (VHS) into Lake Champlain. VHS was first noted in the Great Lakes area in Lake Ontario in 2005, and has since spread to lakes Huron, Michigan, Erie, Ontario and St. Clair, the St. Lawrence River, and inland lakes in New York, Michigan, and Wisconsin (USGS, 2008). As a non-specific pathogen that affects at least 25 fish species, its potential to affect sport fisheries is high. Fish transfers among lakes have been prohibited in an attempt to slow the spread of this pathogen, but fish moving through canals could readily transport VHS into Lake Champlain.

The examples above include only those species that are already in connected waters; additional invaders from elsewhere in North America, Europe, and other parts of the world are still being introduced into the Great Lakes and adjacent waterways, and will pose additional threats to Lake Champlain. For example, the bloody red shrimp (*Hemimysis anomola*) was found in the Great Lakes in 2006 and is now widespread in Lake Ontario (Pothoven et al., 2007).

Prospects for prevention of additional invasions

To protect Lake Champlain, each vector of potential exotic species transfer needs to be addressed: deliberate introductions via stocking, unintentional releases from bait buckets and horticulture (including the increasingly popular water garden trade), trailered boats, and canals. The focus and philosophy of fisheries management has shifted away from the indiscriminant use of exotic species in recent decades, so intentional stocking of new exotic species is highly unlikely. Legislation that restricts sale of non-native bait species in Vermont was passed in 2002. Similar legislation needs to be passed in New York and Quebec to close this pathway. The adoption of the plant quarantine rule in 2002 and follow-up efforts by Agency of Agriculture and VTDEC appear to have removed purple loosestrife from the nursery market in Vermont and reduced sale of a number of other invasive aquatic plants from aquarium and pet stores. Importation of fishes for culture is still a potential source of invasive species; for example, tilapia (*Oreochromis* spp.) are cultured in Vermont. Goldfish are self-sustaining only in a few small private ponds in the basin; they appear periodically in the lake, likely as a result of aquarium dumping.

No amount of legislation will entirely prevent illegal activities, but more stringent oversight may help. Alewife was likely introduced deliberately and illegally into Lake St. Catherine, and tench were imported illegally for aquaculture into Quebec. Tench have already escaped into the Richelieu River due to a breach in a pond dike, and migrated into Lake Champlain. Small numbers of alewife were found in Lake Champlain in 2003, and the population expanded hugely in 2007–2008.

To date no introductions into the state are known to be due to transport on trailered boats, although zebra mussels and aquatic plants have spread into inland lakes in Vermont likely due to this vector. Signs are posted by the state at public launch ramps to inform the public about checking their boats and trailers; periodic inspections by state wardens indicate that boaters do not always heed the instructions to check and clean their boats. Public education to emphasize the problems caused by exotic species, and inform the public about existing legislation and consequences of illegal introductions, is critically important; the Lake Champlain Sea Grant, Lake Champlain Basin Program, Lake Champlain Committee, and VTDEC, among others, have made substantial progress in this area.

The canals remain a major and uncontrolled vector for exotic species introductions into Lake Champlain, as they do in other parts of the country and the world (Aron and Smith, 1971; Mills et al., 1999). Attention is now being directed toward development of a biological barrier on the Champlain Canal. There is historic precedent for this effort: in the 1970s, a decision was made to maintain a marine railway on the Trent-Severn waterway *en lieu* of a lock to prevent passage of sea lamprey from the Great Lakes into Lake Simcoe. In the late 1980s, the Rapide Croche Lock on the Fox River lock system was sealed to prevent entry of sea lamprey into Lake Winnebago from the Great Lakes. Most recently, national attention focused on canals as biological vectors with the installation of an electrical barrier on the Chicago Canal in the 1990s. The original purpose of the barrier was to prevent movement of round goby into the Mississippi River drainage, but this species was already below the barrier when it was put into operation in 2002.

Several strategies to reduce exotic species transfer through the Champlain Canal are possible, including electrical barriers, chemical barriers, filters, bubble curtains, strobes, and acoustic arrays. However, the optimal solution to block the largest number of taxa and the highest proportion of invaders is to separate the watersheds with a physical barrier, as used in the Trent-Severn Canal and Fox River lock system, and accommodate boat traffic by moving it over or around the barrier. A less drastic, but still highly effective solution, would be to open the locks only for occasional large commercial traffic such as barges, while using technology such as a boat hoist for the frequent passage of smaller vessels. Recognition that complete prevention of exotic species introductions may be unrealistic will open discussion of solutions that, instead, minimize the risks.

Acknowledgements

Many individuals contributed to this compilation of information; we are particularly grateful to Ann Bove, Robert Daniels, Mark Ferguson, Steve Fiske, Rich Langdon, and David Strayer for offering their expertise and for their assistance teasing apart records and rumors for this manuscript. This work was stimulated by discussions and brainstorming with Mark Malchoff, Lake Champlain Sea Grant, and was funded by National Sea Grant.

References

- Aiken, S.G., Newroth, P.R., Wile, I., 1979. The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. Can. J. Plant Sci. 59, 201–215.
- Anderson, L.C., Zeis, C.D., Alam, S.F., 1974. Phytogeography and possible origins in North America. Bull. Torrey Bot. Club 101, 292–296.
- Aron, W.I., Smith, S.H., 1971. Ship canals and aquatic ecosystems. Science 174, 13–20.
- Bailey, R.M., Smith, G.R., 1981. Origin and geography of the fish fauna of the Laurentian Great Lakes basin. Can. J. Fish. Aquat. Sci. 38, 1539–1561.
- Ball, I.R., 1969. *Dugesia lugubris* (Tricladia: Paludicola), a European immigrant into North American fresh waters. J. Fish. Res. Bd. Can. 26, 221–228.
- Beekey, M.A., McCabe, D.J., Marsden, J.E., 2004. Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. Oecologia 141, 164–170.
- Bell, R., 1971. Handbook of the Malacostraca of Vermont and neighboring regions (crayfish, sowbugs and their relatives). University of Vermont, Burlington VT, p. 65.
- Benson, A.J., 1999. Documenting over a century of aquatic introductions in the United States. In: Claudi, R., Leach, J.H. (Eds.), Nonindigenous freshwater organisms: vectors, biology, and impacts. Lewis Publishers, Boca Raton FL, pp. 1–31.

- Bernatchez, L., 1997. Mitochondrial DNA analysis confirms the existence of two glacial races of rainbow smelt *Osmerus mordax* and their reproductive isolation in the St. Lawrence River estuary (Quebec, Canada). *Mol. Ecol.* 6, 73–83.
- Bove, A., Hunt, T., Crawford, S., 2002. 1999 Water chestnut management program: Lake Champlain and inland waters in Vermont. Prepared for the Lake Champlain Basin Program, Grand Isle, VT. 25 pp.
- Bradley, L.J., 1931. *Rorippa amphibia* in Fairfield County, Connecticut. *Rhodora* 33, 192–193.
- Brown, E., Duchovnay, A., Shambaugh, A., and Williams, A., 1992. 1991 Lake Champlain Biomonitoring Program. School of Natural Resources, University of Vermont, Burlington VT.
- Brown, E., Duchovnay, A., Shambaugh, A., and Williams, A., 1993. 1992 Lake Champlain Biomonitoring Program. School of Natural Resources, University of Vermont, Burlington VT.
- Bryan, M.B., Zalinski, D., Filcek, K.B., Libants, S., Li, W., Scribner, K.T., 2005. Patterns of invasions and colonization of the sea lamprey (*Petromyzon marinus*) in North America as revealed by microsatellite genotypes. *Mol. Ecol.* 14, 3757–3773.
- Burch, J.B., 1972. Freshwater Sphaeriacean clams (Mollusca: Pelecypoda) of North America. U. S. Govt. Printing Office, Washington DC.
- Burlington Free Press, 1937. Feature story concerning Elsie M. Kittredge. Burlington, VT. December 27:2.
- Carlson, D.M., Daniels, R.A., 2004. Status of fishes in New York: increases, declines and homogenization of watersheds. *Am. Midl. Nat.* 152, 104–139.
- Catling, P.M., Dore, W.G., 1982. Status and identification of *Hydrocharis morus-ranae* and *Limnobium spongia* (Hydrocharitaceae) in northeastern North America. *Rhodora* 84 (840), 523–545.
- Clausen, R.T., 1936. Studies in the genus *Najas* in the northern United States. *Rhodora* 38, 333–335.
- Cody, W.J., 1961. *Iris pseudacorus* L. escaped from cultivation in Canada. *Can. Field Nat.* 75, 139–142.
- Copans, B., Garrity, M., 2003. Vermont's purple loosestrife biological control program, 2003 Annual Report. Vermont Department of Environmental Conservation, Waterbury, VT.
- Countryman, W.D., 1968. *Alisma gramineum* in Vermont. *Rhodora* 70, 577–579.
- Countryman, W.D., 1970. The history, spread and present distribution of some immigrant aquatic weeds in New England. *Hyacinth Control J.* 8, 50–52.
- Countryman, W.D., 1975. Lake Champlain's Inland Sea and the distribution of aquatic plants. Proceedings of the Lake Champlain Basin Environmental Conference, Chazy, NY. 85–91.
- Countryman, W.D., 1978. Nuisance aquatic plants in Lake Champlain. Lake Champlain Basin Study. Prepared for the Eutrophication Task Force, Burlington, VT. 102 pp.
- Couture, S.C., Watzin, M.C., 2008. Diet of invasive adult white perch (*Morone americana*) and their effects on the zooplankton community in Missisquoi Bay, Lake Champlain. *J. Great Lakes Res.* 34, 485–494.
- Crocker, D.W., 1957. The crayfishes of New York State (Decapoda, Astacidae). *N.Y. Mus. Sci. Serv.* 355, 1–97.
- Daniels, R.A., 2001. Untested assumptions: the role of canals in the dispersal sea lamprey, alewife, and other fishes in the eastern United States. *Env. Biol. Fish.* 60, 309–329.
- Daniels, R.A., Murphy, D.C., Klemmens, M.W., 2001. *Orconectes neglectus* is established in the northeast. *Northeastern Nat.* 8, 93–100.
- DeKay, J.E., 1842. The New York fauna. Division II. Invertebrated animals. Class VI. Mollusca, part 5. Zoology of New York, or the New York Fauna. Natural History of New York. Albany, NY. 271 pp.
- de Lafontaine, Y., Costan, G., 2002. Introduction and transfer of alien aquatic species in the Great Lakes–St. Lawrence River basin. In: Caudi, R., Nantel, P., Muckle-Jeffs, E. (Eds.), Alien invaders in Canada's waters, wetlands, and forest. Natural Resources Canada, Ottawa, Ontario, pp. 103–110.
- Dermott, R., Legner, M., 2002. Dense mat-forming bacterium *Thioploca ingrica* (Beggiatoaceae) in eastern Lake Ontario: implications to the benthic food web. *J. Great Lakes Res.* 28, 688–697.
- Duchovnay, A., Reid, J.W., McIntosh, A., 1992. *Thermocyclops crassus* (Crustacea: Copepoda) present in North America: a new record from Lake Champlain. *J. Great Lakes Res.* 18, 415–419.
- Eggleston, W.W., 1904. Addenda to the flora of Vermont. *Rhodora* 6, 137–144.
- Eliopoulos, K., and Stangel, P., 1999. Lake Champlain 1998 zebra mussel monitoring program. Final Report. VTDEC, Waterbury, VT 32 pp.
- Eliopoulos, K., and Stangel, P., 2001. Lake Champlain 2000 zebra mussel monitoring program. Final Report. VTDEC, Waterbury, VT
- Emery, L., 1985. Review of fish species introduced into the Great Lakes, 1819–1974. Great Lakes Fishery Commission Technical Report No. 45, Ann Arbor MI.
- ERDC (Engineer Research and Development Center), UNDATED. *Myriophyllum aquaticum* (Vell.) Verdc. (Parrotfeather) U.S. Army Corps of Engineers: Noxious and Nuisance Plant Management Information System.
- Evermann, B.W., Kendall, W.C., 1902. An annotated list of fishes known to occur in Lake Champlain and its tributaries. U. S. Commission of Fish and Fisheries. Commission Report for 1901 pages 217–225.
- Faber, D.J., Jermolajev, E.G., 1966. A new copepod genus in the plankton of the Great Lakes. *Limnol. Oceanog.* 11, 301–303.
- Fichtel, C., Smith, D.G., 1995. The freshwater mussels of Vermont. Leahy Press, Montpelier, VT, p. 54.
- Fisheries Technical Committee, 2008. Strategic Plan for Lake Champlain Fisheries. Lake Champlain Fish and Wildlife Management Cooperative, USFWS, Essex Junction, VT
- Fiske, S., Levey, R., 1996. Survey of native mussel beds in Lake Champlain 1995. Vermont Agency of Natural Resources, Waterbury, VT.
- Fitzsimons, J.D., Brown, S.B., Honeyfield, D.C., Hnath, J.G., 1999. A review of early mortality syndrome in Great Lakes salmonids and its relationship with thiamine deficiency. *Ambio* 28, 9–15.
- Fuller, P.L., Nico, L.G. Williams, J.D., 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society, Special Publication 27, Bethesda, MD.
- Gaiser, L.O., 1949. Further distribution of *Butomus umbellatus* in the Great Lakes region. *Rhodora* 51, 385–390.
- Good, S., Cargelli, L., 2001. Alternative strategies for the management of non-indigenous alewives in Lake St. Catherine, Vermont. VT Dept. of Fish and Wildlife, Pittsford, VT
- Greeley, J.R., 1930. Fishes of the Lake Champlain watershed. Pp. 48–87 In: F. Moore (ed.) A biological survey of the Champlain watershed. Supplement to the 19th annual report of the New York State Conservation Department, Albany, NY
- Greeley, J.R., 1965. Eradication of water chestnut. *Conservationist* 19, 13–15.
- Greene, C.W., 1930. The smelts of Lake Champlain. pp. 105–129 In: F. Moore (ed.) A biological survey of the Champlain watershed. Supplement to the 19th annual report of the New York State Conservation Department, Albany, NY
- Halnon, L.C., 1954. Population study of some of the game, non-game, and forage fish species associations in Lake Champlain. Job completion report F-1-R-3 Job 5, Vermont Fish and Game Department, Essex Junction, VT. 29 pp.
- Halnon, L.C., 1963. Historical survey of Lake Champlain's fishery. Vermont Fish and Game Job Completion Report F-1-R-10 Job 6. Vermont Fish and Game Department, Essex Junction, VT. 96pp.
- Harman, W.N., 1968. Replacement of pleurocerids by *Bithynia* in polluted waters of central New York. *Nautilus* 81, 77–83.
- Hawes, E.J., Parrish, D.L., 2003. Factors affecting the expansion of white perch in Lake Champlain. *J. Great Lakes Res.* 29, 268–279.
- Henson, E.B., Potash, M., 1970. Limnology of Lake Champlain, 1965–1970: a compilation report to the Office of Water Resources Research, Department of the Interior. University of Vermont, Burlington, VT, 23 pp.
- Hummel, M., Kiviak, E., 2004. Review of world literature on water chestnut with implications for management in North America. *J. Aquatic Plant Manage* 42, 17–28.
- Hunt, T., Crawford, S., 2003. 2002 Water chestnut management program: Lake Champlain and inland waters in Vermont. Prepared for the Lake Champlain Basin Program, Grand Isle, VT. 39 pp.
- Hunt, T., Marangelo, P., 2005. 2004 Water chestnut management program: Lake Champlain and inland waters in Vermont. Prepared for the Lake Champlain Basin Program, Grand Isle, VT. 37 pp.
- Janssen, J., Jude, D.J., 2001. Recruitment failure of the mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *J. Great Lakes Res.* 27, 319–328.
- Jokinen, E.H., 1992. The freshwater snails (Mollusca: Gastropoda) of New York State. *New York State Museum Bulletin* 482, Albany NY.
- Johnson, R.I., 1945. *Radix auricularia*. *Nautilus* 58, 144–145.
- Kamman, N., 1994. Lake Champlain long-term water quality and biological monitoring project: zebra mussel monitoring component. Final Report. VTDEC, Waterbury, VT
- Keast, A., 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their macroinvertebrate prey. *Can. J. Zool.* 62, 1289–1303.
- Knowlton, C.H., 1923. *Butomus umbellatus* on the St. Lawrence River. *Rhodora* 25, 220–221.
- Lake Champlain Basin Program, 2005. Lake Champlain Basin Aquatic Nuisance Species Management Plan. Grand Isle, VT. 80 pp.
- Langdon, R.W., Ferguson, M.T., Cox, K.M., 2006. Fishes of Vermont. Vermont Department of Fish and Wildlife, Waterbury, VT.
- Levri, E.P., Kelly, A.A., Love, E., 2007. The invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in Lake Erie. *J. Great Lakes Res.* 33, 1–6.
- Lumsden, H.G., McLaughlin, D.J., 1988. European frog-bit, *Hydrocharis morsus-ranae*, in Lake Ontario marshes. *Can. Field Nat.* 102, 261–263.
- MacIsaac, H.J., Grigorovich, I.A., Hoyle, J.A., Yan, N.D., Panov, V.E., 1999. Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran *Cercopagis pengoi*. *Can. J. Fish. Aquat. Sci.* 56, 1–5.
- Mackie, G.L., Quadri, S.U., 1971. A polychaete, *Manayunkia speciosa*, from the Ottawa River, and its North American distribution. *Can. J. Zool.* 49, 760–762.
- Madsen, J.D., Sutherland, J.W., Bloomfield, J.A., Eichler, L.W., Boylen, C.W., 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. *J. Aquatic Plant Manage* 29, 94–99.
- Makarewicz, J.C., Grigorovich, I.A., Mills, E., Damaske, E., Cristescu, M.E., Pearsall, W., LaVoie, M.J., Keats, R., Rudstam, L., Hebert, P., Halbritter, H., Kelly, T., Matkovich, C., MacIsaac, H.J., 2001. Distribution, fecundity, and genetics of *Cercopagis pengoi* (Ostroumov) (Crustacea, Cladocera) in Lake Ontario. *J. Great Lakes Res.* 27, 19–32.
- Mandrak, N.E., Crossman, E.J., 1992. Postglacial dispersal of freshwater fishes into Ontario. *Can. J. Zool.* 70, 2247–2259.
- Marie-Victorin, É.C., 1964. *Flore Laurentienne*. 2nd edition, revised by E. Rouleau. Les Presses de l'Université de Montréal, Montréal
- Marsden, J.E., Langdon, R.W., Good, S.P., 2000. First occurrence of the brook silverside, *Labidesthes sicculus* (Cope), in New England. *Northeastern Nat.* 7, 248–254.
- Marsden, J.E., Chipman, B.D., Nashett, L.J., Anderson, J.K., Bouffard, W.B., Durfey, W., Gersmehl, J.E., Schoch, W.F., Staats, N.R., Zerrenner, A., 2003. Sea lamprey control in Lake Champlain. *J. Great Lakes Res.* 29 (suppl. 1), 655–676.
- McKibben, A., McKibben, S., 1997. Cruising guide to Lake Champlain: the waterway from New York City to Montreal. Lake Champlain Publishing Co., Burlington VT.
- Mehrhoff, L.J., Silander, J.A., Leicht, S.A., Mosher, E., 2003. IPANE: Invasive Plant Atlas of New England. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA.

- Merilainen, J., 1968. *Najas minor* All. in North America. *Rhodora* 70, 161–175.
- Mills, E.L., Chrisman, J.R., Holeck, D.T., 1999. The role of canals in the spread of nonindigenous species in North America. In: Claudi, R., Leach, J.H. (Eds.), *Nonindigenous freshwater organisms: vectors, biology, and impacts*. Lewis Publishers, Boca Raton, FL, pp. 347–380.
- Mills, E.L., Leach, J.H., Carlton, J.T., Secor, C.L., 1993. Exotic species in the Great Lakes – a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* 19, 1–54.
- Mills, E.L., Strayer, D.L., Scheierell, M.D., Carlton, J.T., 1996. Exotic species in the Hudson River Basin: a history of invasions and introductions. *Estuaries* 19, 814–823.
- Minshall, W.H., 1940. Frog-bit *Hydrocharis morsus-ranae* L. at Ottawa. *Can. Field-Nat.* 54, 44–45.
- Moore, E., (ed.) 1930. A biological survey of the Champlain watershed. Supplement to the 19th annual report of the New York State Conservation Department, Albany, NY
- Muenschler, W.C., 1930a. Aquatic vegetation of the Lake Champlain watershed. A biological survey of the Champlain watershed. Supplemental to Nineteenth Annual Report, 1930. New York State Conservation Department, NY, pp. 164–185.
- Muenschler, W.C., 1930b. *Butomus umbellatus* in the Lake Champlain basin. *Rhodora* 32, 19–20.
- Muenschler, W.C., 1935. Aquatic vegetation of the Mohawk watershed. In: Moore, E. (Ed.), *A biological survey of the Mohawk–Hudson watershed. Supplement to 24th Annual Report of the New York State Conservation Department*. Albany, NY, pp. 228–249.
- Muzinic, C.J., 2000. First record of *Daphnia lumholzi* Sars in the Great Lakes. *J. Great Lakes Res.* 26 (3), 352–354.
- Myer, G.E., Gruendling, G.K., 1979. Limnology of Lake Champlain. *Lake Champlain Basin Study*, Burlington VT.
- Norton, A.H., 1933. *Rorippa amphibia* in Androscoggin County, Maine. *Rhodora* 33, 262.
- Olsen, T.M., Lodge, D.M., Capelli, G.M., Houlihan, R.J., 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can. J. Fish. Aquat. Sci.* 48, 1853–1861.
- Page, C.W., 1969. Aquatic diptera in Lake Champlain embayments. MS Thesis, University of Vermont, Department of Zoology, 101pp.
- Plösch, D.S., Nashett, L.J., 1990. First reported occurrence of white perch in Lake Champlain. New York State Department of Environmental Conservation, Bureau of Fisheries, Albany, NY, 4pp.
- Pothoven, S.A., Grigorovich, I.A., Fahnenstiel, G.L., Balcer, M.D., 2007. Introduction of the Ponto-Caspian bloody-red mysid *Hemimysis anomala* into the Lake Michigan basin. *J. Great Lakes Res.* 33 (1), 285–292.
- Raymond, M., Kucyniak, J., 1948. Six additions to the adventitious flora of Quebec. *Rhodora* 50, 176–180.
- Ricciardi, A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity Distrib.* 12, 425–433.
- Ricciardi, A., Reiswig, H.M., 1994. Taxonomy, distribution, and ecology of the freshwater bryozoans (Ectoprocta) of eastern Canada. *Can. J. Zool.* 72, 339–359.
- Rogick, M.D., 1934. Studies on fresh-water bryozoa. I. The occurrence of *Lophopodella carteri* (Hyatt) 1866 in North America. *Trans. Am. Microscop. Soc.* 53, 416–424.
- Saltonstall, K., 2002. Cryptic invasion by non-native genotypes of the common reed, *Phragmites australis*, into North America. *Proc. Natl. Acad. Sci.* 99, 2445–2449.
- Schaeffer, J.S., Margraf, F.J., 1987. Predation on fish eggs by white perch, *Morone americana*, in western Lake Erie. *Envir. Biol. Fish.* 18, 77–80.
- Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. *Bull. Fish. Res. Bd. Can.* 184 966pp.
- Simpson, K.W., Abele, L.A., 1984. *Ribistes parasita* (Schmidt) (Oligochaeta: Naiadidae), a distinctive oligochaete to North America. *Freshwat. Invert. Biol.* 3, 36–41.
- Smith, S.H., 1970. Species interactions of the alewife in the Great Lakes. *Trans. Amer. Fish. Soc.* 4, 754–765.
- Smith, D.G., 1983. Notes on Mississippi River basin Mollusca presently occurring in the Hudson River system. *Nautilus* 97, 128–131.
- Smith, D.G., 1985a. A study of the distribution of freshwater mussels (Mollusca: Pelecypoda: Unionoidea) of the Lake Champlain drainage in northeastern New England. *Am. Midl. Nat.* 114, 19–29.
- Smith, C.L., 1985b. The inland fishes of New York State. New York State Department of Environmental Conservation, Albany NY, 522 pp.
- Smith, D.G., 1986. *Pisidium henslowanum* (Sheppard) in the Connecticut River, Massachusetts (Bivalvia: Pisidiidae). *Nautilus* 100, 124–126.
- Smith, D.G., 2000. Notes on the taxonomy of introduced *Bellamyia* species in northeastern North America. *Nautilus* 114, 31–37.
- Sonstegard, R.A., Hnath, J.G., 1978. Lymphsarcoma in muskellunge and northern pike: guidelines for disease control. *Am. Fish. Soc. Spec. Publ.* 11, 235–237.
- Soper, E., 1993. They're here – just what does this mean for Lake Champlain? *Casin' the Basin* (Lake Champlain Basin Program, Grand Isle, VT) 1(5):1, 4–5.
- Spaulding, S., and Elwell, L., 2007. Increase in nuisance blooms and geographic expansion of the freshwater diatom *Didymosphenia geminata*: recommendations for response. USEPA white paper, <http://www.epa.gov/region8/water/didymosphenia/>.
- Stickney, M., 1996. Lake Champlain 1995 zebra mussel monitoring program. Final Report. Vermont Dept. of Environmental Conservation, Waterbury, VT
- Strayer, D.L., 1987. Ecology and zoogeography of the freshwater mollusks of the Hudson River basin. *Malcolg. Rev.* 20, 1–68.
- Strayer, D.L., 2006. Alien species in the Hudson River. In: Levinton, J.S., Waldman, J.R. (Eds.), *The Hudson River Estuary*. Cambridge University Press, pp. 296–310.
- Sutherland, W.J., 1990. Biological flora of the British Isles, No. 169. *Iris pseudacorus*. *J. Ecol.* 78, 833–848.
- Taylor, C.A., Schuster, G.A., Cooper, G.A., DiStefano, R.J., Eversole, A.G., Hamr, P., Hobbs III, H.H., Robison, H.W., Skelton, C.E., Toma, R.F., 2007. A reassessment of the conservation status crayfishes of the United States and Canada after 10+ years of increased awareness. *Fisheries* 32, 372–389.
- Thompson, Z., 1853. *Natural History of Vermont*. C. E. Tuttle Co, Rutland, VT.
- Thompson, F.G., 1984. North American freshwater snail genera of the hydrobiid subfamily Lithoglyphinae. *Malacologia* 25, 109–141.
- Thompson, D.Q., Stuckey, R.L., Thompson, E.B., 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. U.S. Dept. of the Interior. Fish and Wildlife Service, Springfield, VA, 55 pp.
- Underhill, J.C., 1986. The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland and Labrador. In: Hocutt, C.H., Wiley, E.O. (Eds.), *Zoogeography of North American fishes*. John Wiley and Sons, New York, pp. 106–136.
- USDA-NRCS (United States Department of Agriculture-Natural Resources Conservation Service) 2002. *Potamogeton crispus* L. The PLANTS Database, Version 3.5 [Online Database] National Plant Data Center, Baton Rouge, USA.
- United States Fish and Wildlife Service (USFWS), 2003. The Erie Canal and introduced species. Lower Great Lakes Fishery Resources Office, Amherst, NY, 2pp.
- United States Geological Survey (USGS), 2008. Molecular Epidemiology of Viral Hemorrhagic Septicemia Virus in the Great Lakes Region. URL: <http://wfrc.usgs.gov/pubs/factsheetpdf/vhsfs2011108.pdf>. Accessed Oct 23, 2008.
- Vachon, N., Dumont, P., 2000. Study of the first references to tench (*Tinca tinca* L.) caught in the upper-Richelieu River (Quebec). Quebec Society of Wildlife and Parks, Monteregie Directorate of Wildlife Management, Longueuil, Technical Report 16–07.
- Verdon, R., Desrochers, D., Dumont, P., 2003. Recruitment of American eels in the Richelieu River and Lake Champlain: provision of upstream passage as a regional-scale solution to a large-scale problem. In: Dixon, D.A. (Ed.), *Biology, management, and protection of catadromous eels*. American Fisheries Society, Bethesda, MD, pp. 125–138.
- Waldman, J.R., Grunwald, C., Roy, N.K., Wirgin, I., 2004. Mitochondrial DNA analysis indicates sea lampreys are indigenous to Lake Ontario. *Trans. Am. Fish. Soc.* 133, 950–960.
- Weldy, T., Werier, D., 2005. New York Flora Atlas. [S. M. Landry and K. N. Campbell (original application development), Florida Center for Community Design and Research. University of South Florida]. New York Flora Association, Albany, New York.
- Witt, J.D.S., Herbert, P.D.N., Morton, W.B., 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. *Can. J. Fish. Aquat. Sci.* 54, 264–268.
- Zaranko, D.T., Farara, D.G., Thompson, F.G., 1997. Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). *Can. J. Fish. Aquat. Sci.* 54, 809–814.
- Zilliox, R.G., Youngs, W.D., 1958. Further studies on the smelt of Lake Champlain. *N. Y. Fish Game J.* 5, 165–174.