

European Valve Snail *Valvata piscinalis* (Müller) in the Laurentian Great Lakes Basin

Igor A. Grigorovich^{1,*}, Edward L. Mills², Carl B. Richards³,
Dan Breneman⁴, and Jan J.H. Ciborowski⁵

¹*Department of Fisheries and Wildlife Sciences
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061*

²*Department of Natural Resources
Cornell Biological Field Station
Bridgeport, New York 13030*

³*Minnesota Sea Grant
University of Minnesota-Duluth
Duluth, Minnesota 55812*

⁴*Natural Resources Research Institute
University of Minnesota-Duluth
Duluth, Minnesota 55811*

⁵*Department of Biological Sciences and Great Lakes Institute for Environmental Research
University of Windsor
Windsor, Ontario N9B 3P4*

ABSTRACT. Previously reported from the lower Great Lakes basin and St. Lawrence and Hudson rivers, the nonindigenous gastropod *Valvata piscinalis* was found for the first time in Superior Bay (Minnesota) of Lake Superior, Lake Michigan (Wisconsin), and Oneida Lake (New York) of the Lake Ontario basin. This snail was not abundant in Lakes Superior and Michigan, whereas in eutrophic Oneida Lake it reached a maximum density of 1,690 individuals/m² (mean density = 216 individuals/m²). Human-mediated disturbances could facilitate the range extension of this snail by providing dispersal opportunities (e.g., canals, shipping traffic) or increasing nutrients (e.g., eutrophication). A native of the Palaearctic region, *V. piscinalis* has colonized sites across the Great Lakes basin, suggesting that it will likely become common in disturbed Great Lakes areas.

INDEX WORDS: *Valvata piscinalis*, European valve snail, nonindigenous species, Lake Superior, Lake Michigan, Oneida Lake.

INTRODUCTION

Valvata piscinalis (Müller 1774) is a freshwater gastropod (family Valvatidae) whose native range encompasses Europe, Caucasus, western Siberia, and Central Asia. The species is widely distributed and common in European freshwaters (Zhadin

1965, Anistratenko 1998). It typically inhabits standing and slightly flowing waters. The construction of canals and reservoirs permitted *V. piscinalis* to spread in the former Soviet Union (Shevtsova 1991), although its invasion history has not been well documented. The European valve snail was first recorded [as *V. obtusa*] in North America in Lake Ontario near the mouth of the Genesee River, New York, in 1897, where it reached high densities within a few years (Baker 1898, 1900). Four decades later, the snail had dispersed into Lake Erie

*Corresponding author. Present address: 320 Dixon Road, Suite 1016,
Toronto, Ontario M9R 1S8. E-mail: IgorGrigorovich@yahoo.ca

and since then has colonized the neighboring St. Lawrence and Hudson rivers and inland lakes Champlain and Cayuga (Oughton 1938, Robertson 1945, Harman 1968, Jokinen 1992, Strayer 1999).

There have been a number of accounts of the distribution of *V. piscinalis* in North America (Baker 1898, 1900; Latchford 1914; Oughton 1938; Mackie *et al.* 1980; Clarke 1981). Yet, the range and the patterns of spread of this species in North America remain inadequately studied. The dispersal of *V. piscinalis* in the Great Lakes has been restricted and characterized by a slow rate of spread during the first 100 years of the colonization. Its slow range expansion contrasts with the invasion of the Great Lakes by the Ponto-Caspian molluscs *Dreissena polymorpha* and *D. bugensis*. Since their discovery in the late 1980s, these species have rapidly expanded their distributions in this basin (e.g., Mills *et al.* 1993, Vanderploeg *et al.* 2002). In this study, we describe new records of *V. piscinalis* in the Great Lakes basin. In order to comprehend the range of habitats that *V. piscinalis* may invade in the Great Lakes, we review aspects of the species' life history, ecology, and distribution in Eurasia and North America.

METHODS AND MATERIALS

Benthic samples examined for the presence of *V. piscinalis* were collected at the following locations in the Great Lakes basin: St. Louis River and Bay and Superior Bay of Lake Superior, June 1995 (Fig. 1, inset map; see Breneman *et al.* 2000 for details); nine littoral areas around the perimeter of Lake Superior, June and August 2001 (see Grigorovich *et al.* 2003 for details); the southern shoreline of Lake Superior, July–September 2002 and June–July 2003; St. Clair River, Lake St. Clair, Detroit River, western Lake Erie, and western Lake Ontario, August–October 1997 and May–October 1998 (Fig. 1, inset map; see Grigorovich *et al.* 2000 for details); littoral (20–50 cm) and deeper-water (5–10 m) sites around the perimeter of Lakes Huron and Michigan, July and August 2002 and August 2003; western Lake Erie, June 2002 and June 2003 (see supplementary material available from http://filebox.vt.edu/users/igorg/Appendix-Valvata_piscinalis_in_the_Great_Lakes_basin.pdf for details). Samples were also obtained from 15 sites on Oneida Lake during August 2002 (Fig. 1, inset map). This inland lake is connected to Lake Ontario through the Oswego River.

Collections were made using a Petite ponar grab

(area 225 cm²; 2–5 grabs per location) and/or bottom sled dredge (width 0.38 m, mesh 500 μ m; duration 7–12 min, depending on volume of material retrieved). In the St. Louis River area, mollusks were also collected using a cylindrical drop core (area 13 cm²; typically 12 or more per site). Shallow-water sites in the Lake Huron-Lake Erie corridor were also sampled for molluscs by sweeping a D-frame dip net (mesh 500 μ m; 30-s traveling sweeps at 20-cm and 50-cm depths at 2–6 locations per site) through vegetation, rocks, and debris.

Most sites were situated in the near-shore zone (< 4 km from shore) at depths up to 20 m. At offshore sites, depths ranged from 7 to 64 m. Surveyed bottom substrates included mud, silt, sand, gravel, pebbles, and boulders. All samples were preserved in 70% ethanol or in 4–10% formalin.

In the laboratory, *V. piscinalis* was separated from other material, measured (to the nearest 0.01 mm), and enumerated under a dissecting microscope. All specimens were identified by I.A. Grigorovich.

Representative voucher specimens of *V. piscinalis* from Lake Superior and Oneida Lake have been deposited in the Canadian Museum of Nature, Ottawa, Ontario (entire specimens preserved in ethanol; catalogue numbers CMNML 093773 and CMNML 093774); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (shells); and the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine (shells and viscera preserved in ethanol).

RESULTS AND DISCUSSION

Valvata piscinalis was found at three new locations beyond its previously reported distribution in the Great Lakes—Superior Bay (Minnesota), Lake Michigan (Wisconsin), and Oneida Lake (New York) (Fig. 1). Living *V. piscinalis* individuals were present at four littoral sites sampled in Superior Bay in 1995. Water depths at these sites were 1.4 and 7.7 m. The bottom was overlain with fine-grained sediments including mud, silt, and sand. No living individuals of *V. piscinalis* were found at seven other littoral areas of Lake Superior sampled in 2001. However, empty shells of *V. piscinalis* were detected at a littoral site adjacent to Thunder Bay, Ontario (I. Grigorovich, unpubl. data). Living *V. piscinalis* specimens were also found at a soft-bottomed site that was 8.8 m deep in the southern basin of Lake Michigan off Butt Creek in August 2002 (Fig. 1). *Valvata piscinalis* was also present at

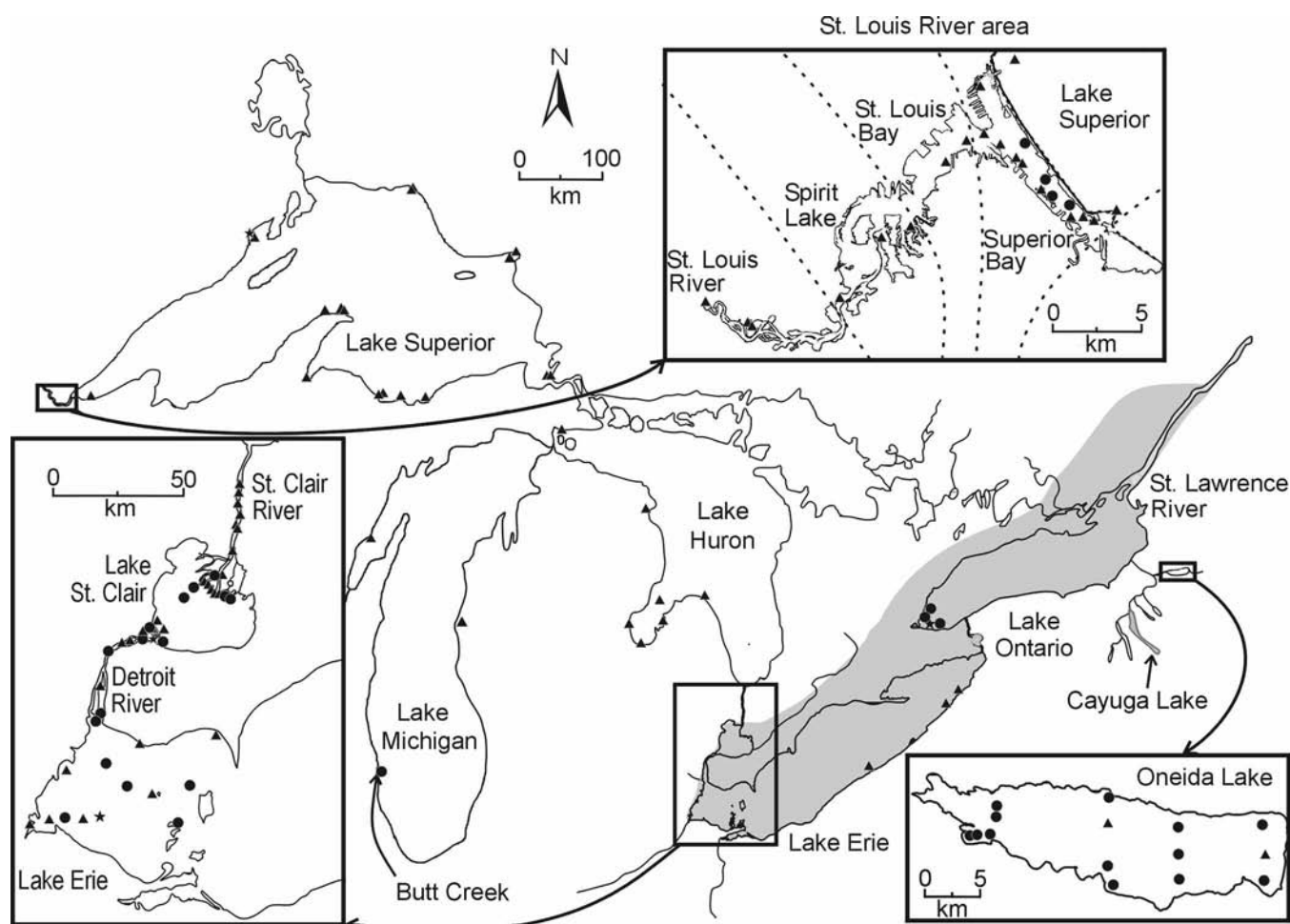


FIG. 1. Geographic distribution of *Valvata piscinalis* in the Laurentian Great Lakes basin. The St. Louis River area is delineated into distinct habitat areas after Breneman et al. (2000). Shaded areas represent previously reported range (modified after Clarke 1981) and symbols indicate recent sampling sites: circles = living specimens collected, stars = empty shells collected, triangles = *V. piscinalis* absent.

numerous localities within its previously reported range in the lower Great Lakes (Fig. 1). These findings indicate that the European valve snail has spread across the Great Lakes basin. The non-gradual pattern in its recent dispersal through the upper lakes suggests that this species takes advantage of human-mediated transport vectors.

During August 2002, *V. piscinalis* was detected at 13 of 15 sites in Oneida Lake. It was present on various bottom substrates including mud, silt, detritus of plant origin, and zebra mussel shell fragments, at a depth range of 3.4 to 13.2 m. Maximum density was observed in shallow water (3.7–4.4 m deep) overgrown by submerged aquatic macrophytes, but no significant linear relationship between population density and depth was found (R^2

= 0.33, $P > 0.05$). Mean and maximum depths of the Great Lakes sites observed to support *V. piscinalis* were 7.3 and 20.5 m, respectively.

Connected with Lake Ontario, Oneida Lake has been invaded by a number of exotic molluscan species since the early 1800s (Harman 2000). It is possible that *V. piscinalis* cryptically invaded this lake some time ago, but its presence was not recognized, probably due to the species' superficial resemblance to the North American *V. sincera*.

Valvata piscinalis is readily distinguished from *V. sincera* by a unique combination of shell features. *Valvata piscinalis* typically possesses an angulated or pinched aperture that is appressed to the penultimate whorl (Fig. 2A), whereas the aperture of *V. sincera* is round and is not pressed to the pre-

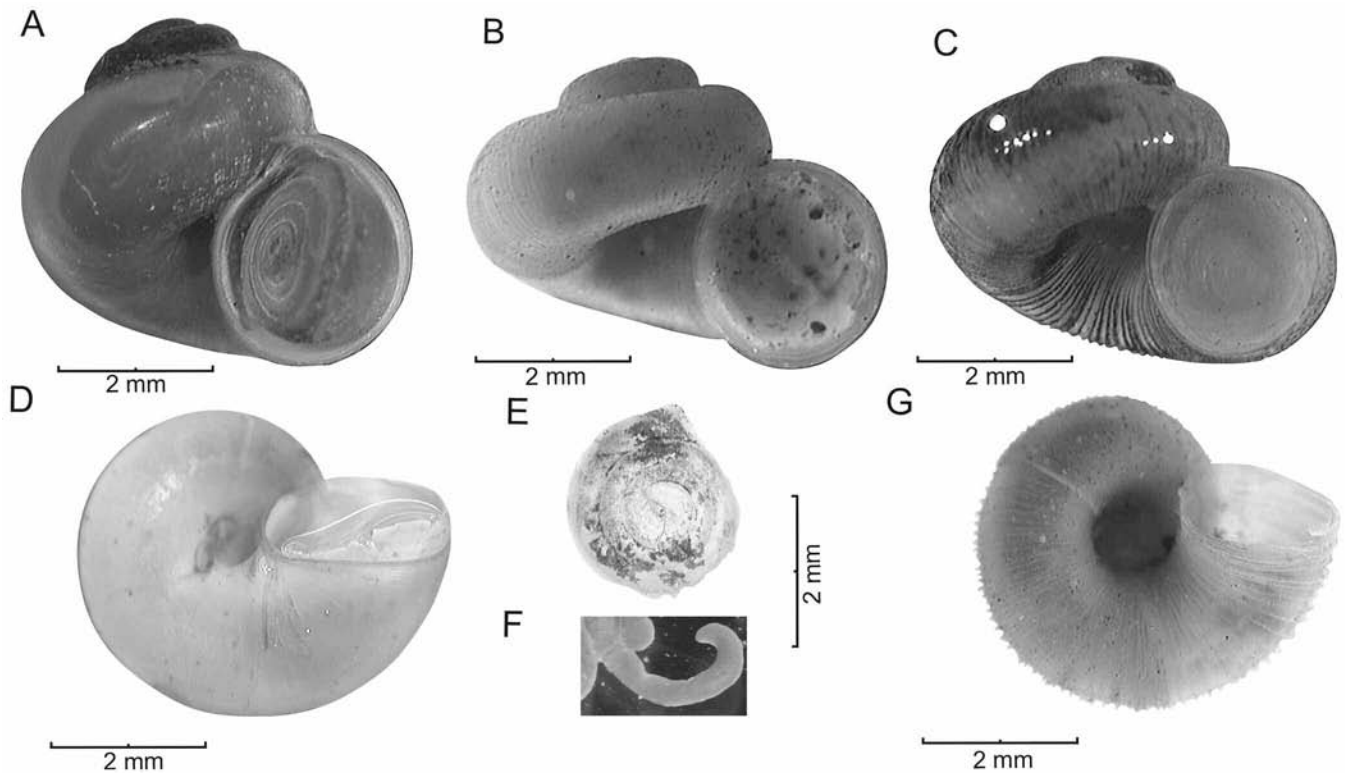


FIG. 2. Morphological features of Valvatidae from the Great Lakes. *Valvata piscinalis* from Oneida Lake: apertural (A) and umbilical (D) views of shell, operculum (E), and copulatory organ (F). *Valvata sincera* from Lake Superior: morph *sincera*, apertural view of shell (B); morph *lewisi*, apertural (C) and umbilical (G) views of shell. Characters useful for recognition of *V. piscinalis*: relatively high spire, well-rounded whorls, angulated aperture, and narrow umbilicus.

ceding whorl (Fig. 2B, C). *Valvata piscinalis* has an umbilicus that is relatively narrow and partly obscured by a reflected inner lip (Fig. 2A, D), while the umbilicus of *V. sincera* is wide and round (Fig. 2G). The spire in *V. piscinalis* is attenuate, while that of *V. sincera* is conical. The growth lines in *V. piscinalis* are fine and dense (Fig. 2A), whereas those in *V. sincera* are widely spaced, sometimes coarse or furnished with blade-like lamellae (Fig. 2B, C).

Valvata piscinalis differs from *V. sincera* by its relatively higher spire and narrower umbilicus (Clarke 1981). However, height of the spire and size of the umbilicus in *V. piscinalis* varies among localities (Zhadin 1965, Fretter and Graham 1978). This variation has been linked to the degree of eutrophication (Fretter and Graham 1978). Our observations support this hypothesis as adults of *V. piscinalis* collected from eutrophic Oneida Lake had a relatively higher spire and a narrower umbilicus than specimens collected in other Great Lakes

locations. In Oneida Lake, individuals of *V. piscinalis* with a shell length of 3.1–4.9 mm strongly dominated, accounting for 69% of the population ($n = 45$) during August 2002 (Fig. 3). In Superior Bay, specimens with 4–5 whorls had a shell up to 5 mm high and 5 mm wide.

Single individuals of *V. piscinalis* were encountered in samples from Superior Bay and Lake Michigan off Butt Creek. The density of *V. piscinalis* in Oneida Lake averaged 216 individuals/m² (SD = 310, $n = 34$). Development of abundant populations of this species in productive habitats has been linked to its high growth rate, elevated reproductive capacities, and efficient feeding strategies (Table 1). For example, in eutrophic Lake Sevan, Armenia, densities can exceed 600 individuals/m² (Ostrovsky 1981). In nutrient-rich environments, this snail, in addition to grazing on epiphytic algae and detritus, consumes suspended organic matter and algae by filter feeding (Tsikhon-Lukanina 1961a, 1961b, 1965).

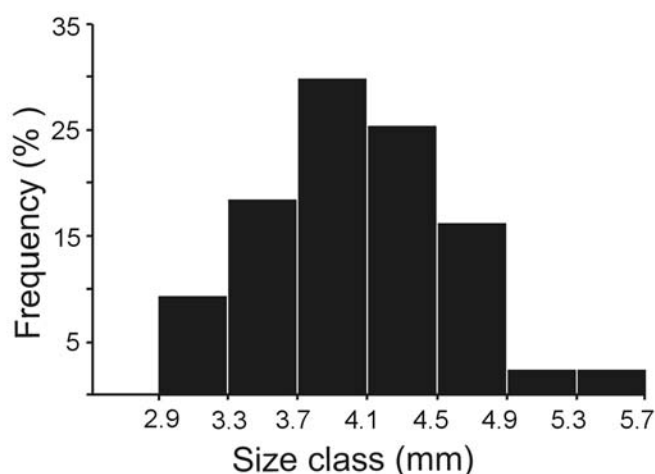


FIG. 3. Length-frequency distribution of *Valvata piscinalis* from Oneida Lake in August 2002. $n = 45$.

Hypothesized general attributes of a successful aquatic invader (e.g., Lodge 1993), including hermaphroditism, high fecundity, rapid growth and maturation, and ability to tolerate adverse environmental conditions, apply well to explain the dispersal and success of the European valve snail in the Great Lakes (Table 1). The Eurasian distribution of *V. piscinalis* has been affected by canals and shipping traffic, as evidenced from frequent sightings of this species in canals and seaways in the former Soviet Union (Grigorovich 1991, Shevtsova 1991).

Apart from human-mediated assistance in dispersing *V. piscinalis*, the species' invasion success can probably be attributed to its fit into the Great

Lakes' milieu (Table 1). It tolerates low calcium waters (Fretter and Graham 1978). The natural range of *V. piscinalis* in continental Europe extends across various landscapes and climatic zones from the arctic to southern arid zones of Europe (Zhadin 1965, Ostrovsky 1981, Olsson 1984, Shevtsova 1991). Its thermal requirements are probably met even in open Lake Superior. *Valvata piscinalis* populates a wide array of habitats including small ponds, streams, canals, large rivers, and lakes (Fretter and Graham 1978, Anistratenko 1998, Shevtsova 1991). The species occurs on a variety of bottom substrates, though it appears to prefer mud and silted sand, where it hibernates during winter (Young 1975). It also frequently occurs on aquatic macrophytes, on which it deposits egg masses. Abiotic conditions of the Great Lakes sites that support and lack *V. piscinalis* were explored to determine whether the species occurs in different types of habitats. No significant differences were found between sites with and without *V. piscinalis* with respect to water depth (Kolmogorov-Smirnov two-sample test, $P > 0.10$). Some differences were noted between sites with and without *V. piscinalis* only with respect to predominant bottom substrates (Table 2). Sites that lacked the species tended to have more hard-bottom substrates. Thus, the lack of records of the European valve snail in St. Clair River and Lake Huron may be related to unfavorable predominant bottom substrates (Table 2). However, the species occurs in similar habitat types in the lower Great Lakes suggesting that all of the Great Lakes are vulnerable to invasion by *V. piscinalis*.

TABLE 1. Characteristics that may facilitate invasion success of *Valvata piscinalis* (based on European studies).

No. Characteristic	Reference
1. Widely distributed and abundant	Zhadin 1965, Ostrovsky 1981, Anistratenko 1998
2. Broad range of habitat types	Fretter and Graham 1978, Ostrovsky 1981, Olsson 1984
3. Wide environmental tolerance; ability to hibernate	Young 1975, Ostrovsky 1981, Olsson 1984
4. Hermaphroditism	Cleland 1954
5. Short life span, typically 13–21 months	Fretter and Graham 1978, Ostrovsky 1981
6. Rapid embryonic (from egg-laying to hatching) and postembryonic growth	Ostrovsky 1981, Hoffmann and Neumann 1990
7. High reproductive capacity: 2–3 spawning periods; each snail can produce up to 150 eggs per spawning	Ostrovsky 1981 Frömming 1956, Fretter and Graham 1978
8. Broad diet; opportunistic feeding by grazing on detritus or filtering	Tsikhon-Lukanina 1961a, 1961b, 1965; Fretter and Graham 1978
9. Commensalism with human activity (e.g., canal development)	Shevtsova 1991

TABLE 2. Comparison of the Great Lakes habitats with and without *Valvata piscinalis* (see https://filebox.vt.edu/users/ligorg/Appendix-Valvata_piscinalis_in_the_Great_Lakes_basin.pdf for details). Bottom substrate types are listed for each habitat in the order of decreasing frequency of occurrence. For the water depth, the values represent the mean and the range.

Habitat/Location	Present			Absent		
	Sampling Effort	Bottom Substrates	Depth (m)	Sampling Effort	Bottom Substrates	Depth (m)
St. Louis River area and Lake Superior	11 ponar samples 56 core samples	silty sand, muddy silt, mud sand	4.3 (0.5–7.8)	93 ponar samples 255 core samples 53 sweeps 3 times of 7 to 10-minute-dredging	mud, silty sand, sand, silt clay, pebbles	10.5 (0.2–64.0)
Lake Michigan	1 ponar sample	silt, detritus, <i>Chara</i>	8.8	9 ponar samples 45 core samples 34 sweeps	mud, silty sand, sand aquatic vegetation, detritus	0.7 (0.4–1.5)
Lake Huron				16 ponar samples 88 core samples 52 sweeps	sand, aquatic vegetation silty sand, mud gravel, boulders	1.2 (0.2–8.3)
St. Clair River				20 ponar samples 9 times of 7 to 10-minute-dredging	silty gravel, <i>Chara</i> zebra mussel shells	7.8(0.5–12.0) other vegetation gravel, mud
Lake St. Clair	4 ponar samples 11 sweeps 8 times of 7 to 10-minute-dredging	silty sand, <i>Chara</i> other vegetation, mud, silt gravel, zebra mussels	3.2(0.5–12.0)	10 ponar samples 15 times of 7 to 10-minute dredging	silty gravel, <i>Chara</i> other vegetation sand, mud	3.8(0.5–12.0)
Detroit River	14 ponar samples 5 sweeps 12 times of 7 to 10-minute-dredging	silty sand, mussel shells gravel, aquatic vegetation	5.2(1.8–11.3)	9 ponar samples 3 sweeps 8 times of 7 to 10-minute-dredging	aquatic vegetation, sand silty gravel, gravel, clay	5.6 (1.5–11.3)
Lake Erie	32 ponar samples 8 times of 7 to 10-minute-dredging	silty sand, zebra mussel shells mud, vegetation gravel, cobble	7.9 (0.5–11.8)	26 ponar samples 56 core samples 32 sweeps 7 times of 7 to 10-minute-dredging	silty sand, mud, clay bedrock, cobble, gravel sand	5.4(0.5–10.4)
Lake Ontario	10 times of 7 to 10-minute-dredging	cobble, silt, bedrock, gravel, zebra mussel shells, bryozoans	17.5 (8.1–22.8)			
Lake Oneida	38 ponar samples	silt, mud zebra mussel shells, detritus	7.0 (3.4–12.0)	6 ponar samples	mud, silt, sand zebra mussel shells	10.7(8.2–13.2)

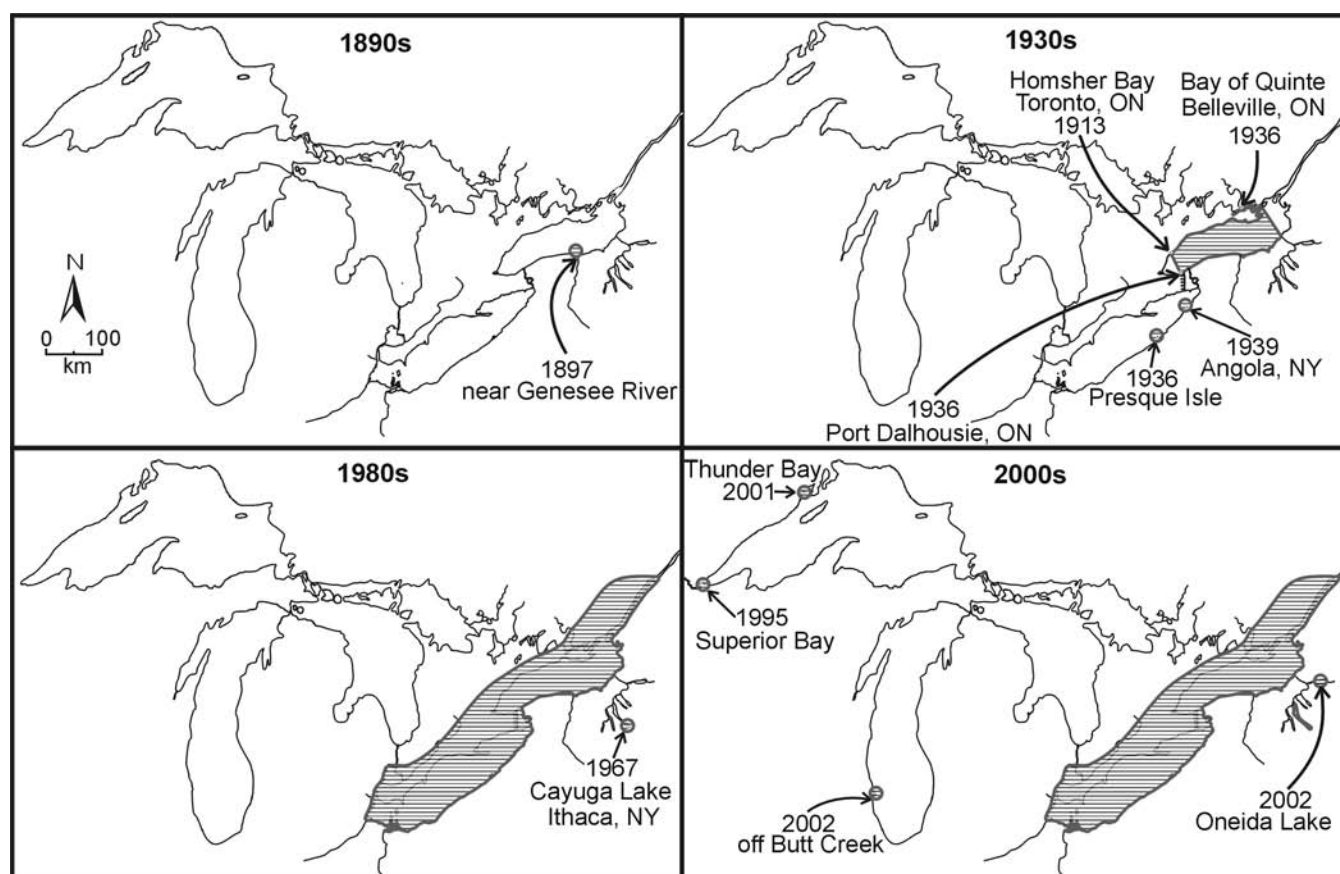


FIG. 4. Map of the Laurentian Great Lakes drainage showing spread of *Valvata piscinalis*. Where available, year of the first observation is indicated for each locality invaded.

Results from our study demonstrate that *V. piscinalis* is more broadly distributed than previously reported in North America. If these recent appearances are not an artifact of earlier misidentifications of *V. piscinalis* as *V. sincera*, then the species' present range and rate of expansion in the Great Lakes basin have increased in recent years compared to the preceding 100 years of its colonization, possibly reflecting changes in vector type. Historical records and our recent collections suggest that the European valve snail exhibited slow, continuous dispersal prior to the 1980s but more rapid, discontinuous dispersal in recent years (Fig. 4). The distributional pattern of *V. piscinalis* in the Laurentian Great Lakes basin consists of isolated colonies in the upper Great Lakes and the inland Finger Lakes, New York, and the lower Great Lakes distribution center from which the species appears to have diffused into surrounding areas. Its appearance in disjunct, restricted localities in Superior

Bay of Lake Superior and in southern Lake Michigan suggests that shipping is a probable vector for *V. piscinalis*. In its native range, *V. piscinalis* frequently occurs in the littoral of large oligotrophic lakes and reservoirs such as Lake Onega, northwestern Russia (e.g., Slepukhina 1975). Considering *V. piscinalis*' environmental tolerances (Table 1), its eventual establishment throughout the upper Great Lakes is anticipated. The ability of *V. piscinalis* to thrive in nutrient-rich habitats associated with catchment land use suggests that this snail will likely continue to invade new areas if humans provide it with additional food resources or dispersal opportunities.

Valvata piscinalis may adversely affect native gastropod communities by competing for food and space. Similar to another introduced snail in the Great Lakes, *Bithynia tentaculata*, *V. piscinalis* is an effective competitor in eutrophic waters, where it can feed on suspended particles (Tsikhon-Lukan-

ina 1961a, 1961b) which are unavailable to native gastropods. The introduction of *B. tentaculata* into Oneida Lake has resulted in displacement of pleurocerid snails (Harman 2000). Similarly, the establishment of the abundant population of *V. piscinalis* has coincided with reduced abundance of native hydrobiid snails in the same lake (I.A. Grigorovich, unpubl. data). Further work is necessary to ascertain the ecological impacts of *V. piscinalis* on native gastropod fauna.

In conclusion, the European valve snail has been able to disperse across the Great Lakes-St. Lawrence River system and invaded several neighboring drainages. Its distributional patterns and appearances in disjunct, restricted localities support the hypothesis that *V. piscinalis* was assisted in its dispersal by humans. If such assistance continues, the species is likely to become a common member of the benthos throughout the Great Lakes.

ACKNOWLEDGMENTS

We thank Vitaliy Anistratenko and Robert Hersher for confirming the identification of *Valvata piscinalis*; Rob Colautti, David Barton, Gerry Mackie, and David Strayer for helpful comments on the manuscript; Travis Spier, Tracy Mabee, and Carolyn Foley for assistance with map data; and Irina Grigorovich for facilitating communication with Ukrainian scientists. This study was supported by the University of Windsor, Cornell University, Michigan Department of Environmental Quality, the U.S. Fish and Wildlife Service, and the U.S. Environmental Protection Agency through its Environmental Monitoring and Assessment Program (EMAP) and Science to Achieve Results (STAR) program (grants R-8286750 and R-828777). The research described in this article has not been subjected to the U.S. Environmental Protection Agency's required peer and policy review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred.

REFERENCES

- Anistratenko, V.V. 1998. Handbook for identification of pectinibranch gastropods of the fauna of Ukraine. Parts 1–2. *Vest. Zool. Suppl.* 8:67–117. (In Russian).
- Baker, F.C. 1898. The molluscan fauna of western New York. *Trans. St. Louis Acad. Sci.* 8:71–94.
- . 1900. Shell collecting near Rochester, N.Y. *Nautilus* 14:69–71.
- Breneman, D., Richards, C., and Lozano, S. 2000. Environmental influences on benthic community structure in a Great Lakes embayment. *J. Great Lakes Res.* 26:287–304.
- Clarke, A.H. 1981. *The freshwater molluscs of Canada*. National Museums of Canada, Ottawa.
- Cleland, D.M. 1954. A study of the habits of *Valvata piscinalis* (Müll.) and the structure and function of the alimentary canal and reproductive system. *Proc. Malacol. Soc. (Lond.)* 30:167–203.
- Fretter, V., and Graham, A. 1978. The prosobranch molluscs of Britain and Denmark. Part 3. Neritacea, Viviparacea, Valvatacea, terrestrial and freshwater Littorinacea and Rissoacea. *J. Moll. Stud. Suppl.* 5:101–152.
- Frömming, E. 1956. *Biologie der mitteleuropäischen Süßwasserschnecken*. Berlin, Germany: Duncker & Humblot.
- Grigorovich, I.A. 1991. On the ecology of molluscs of small rivers in the Dnieper-Donbass Canal system. In *Hydroecological problems of inland waters of Ukraine*, ed. O.M. Arsan, pp. 119–128. Kiev, Ukraine: Naukova dumka. (In Russian).
- , Korniusshin, A.V., and MacIsaac, H.J. 2000. Moitessier's pea clam *Pisidium moitessierianum* (Bivalvia, Sphaeriidae): a cryptogenic mollusc in the Great Lakes. *Hydrobiologia* 435:153–165.
- , Korniusshin, A.V., Gray, D.K., Duggan, I.C., Colautti, R.I., and MacIsaac, H.J. 2003. Lake Superior: an invasion coldspot? *Hydrobiologia* 499:191–210.
- Harman, W.N. 1968. *Valvata piscinalis* in Cayuga Lake, N. Y. *Nautilus* 52:143–144.
- . 2000. Diminishing species richness of mollusks in Oneida Lake, New York State, USA. *Nautilus* 114:120–126.
- Hoffmann, J., and Neumann, D. 1990. Der Lebenszyklus einer niederrheinischen Population von *Valvata piscinalis* (Gastropoda, Prosobranchia). *Decheniana (Bonn)* 143:414–420.
- Jokinen, E.H. 1992. *The freshwater snails of New York State*. New York State Museum, Bull. No. 482, Albany, NY.
- Latchford, F.R. 1914. *Valvata piscinalis* in Canada. *Nautilus* 28:10.
- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8:133–137.
- Mackie, G.L., White, D.S., and Zdeba, T.W. 1980. *A guide to freshwater mollusks of the Laurentian Great Lakes with special emphasis on the genus Pisidium*. Environmental Research Laboratory, U.S. Environmental Protection Agency, Duluth, MN. EPA-600/3-80-068.
- Mills, E.L., Leach, J.H., Carlton, J.T., and 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.
- Olsson, T.I. 1984. Winter sites and cold-hardiness of two

- gastropod species in a boreal river. *Polar Biol.* 3:227–230.
- Ostrovsky, I.S. 1981. Ecological-productional characteristics of a population of *Valvata piscinalis* (Ectobranchia, Valvatidae) in Lake Sevan. *Zool. zh.* 60:825–834. (In Russian).
- Oughton, J. 1938. *Valvata piscinalis* (Müller) in the Great Lakes. *Nautilus* 52:30–32, 60–62.
- Robertson, I.C. 1945. *Valvata piscinalis* (Müller) in Lake Erie. *Nautilus* 59:36.
- Shevtsova, L.V. 1991. *Bottom dwelling animals in the canals of different natural zones*. Kiev, Ukraine: Naukova Dumka. (In Russian).
- Slepukhina, T.D. 1975. Zoobenthos of Lake Onega littoral. In *Littoral zone of Lake Onega*, ed. I.M. Raspopov, pp. 169–182. Leningrad, Russian SFSR: Publishing House Nauka. (In Russian)
- Strayer, D.L. 1999. Effects of alien species on freshwater mollusks in North America. *J. N. Am. Benthol. Soc.* 18:74–98.
- Tsikhon-Lukanina, E.A. 1961a. On the filtration mode of feeding in *Bithynia tentaculata* (L.) and *Valvata piscinalis* (Müller) (Gastropoda, Prosobranchia). *Byul. Inst. biol. vodokhr. akad. nauk SSSR* 10:28–30. (In Russian)
- . 1961b. The dependence of the feeding rate and filtration in some freshwater gastropods on the concentrations of food. *Byul. Inst. biol. vodokhr. akad. nauk SSSR* 10:31–34. (In Russian)
- . 1965. Feeding and growth of freshwater gastropods. *Tr. Inst. biol. vnutr. vod.* 9:191–209. (In Russian.)
- Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 59:1209–1228.
- Young, M.R. 1975. The life cycles of six species of freshwater molluscs in the Worchester-Birmingham Canal. *Proc. Malacol. Soc. (Lond.)* 41:533–548.
- Zhadin, V.I. 1965. *Mollusks of fresh and brackish waters of the USSR. Keys to the Fauna of the USSR published by the Zoological Institute of the Academy Sciences of the USSR, no. 46*. Jerusalem, Israel: Israel Program for Scientific Translations.

Submitted: 13 September 2004

Accepted: 10 February 2005

Editorial handling: David R. Barton