

Another exotic mollusc in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae)

Danuta T. Zaranko, Dennis G. Farara, and Fred G. Thompson

Abstract: In 1991, the hydrobiid snail *Potamopyrgus antipodarum* (Gray 1843), native to New Zealand, was found 1 km offshore Wilson, New York, in Lake Ontario. This is the first known occurrence of the snail in eastern North America. Densities of *P. antipodarum* have increased since its discovery, and the snail is expected to spread quickly throughout the Great Lakes area. The biofouling potential of *P. antipodarum* is probably low; however, its most serious threat may be resource competition with native molluscs. This species was probably introduced in ballast water from transoceanic vessels, thus increasing the list of nonindigenous aquatic organisms introduced into the Great Lakes since the 1800s to 140 different organisms. The risk of other species invasions into the Great Lakes is still possible, despite the now mandatory ballast water regulations.

Résumé : En 1991, l'escargot *Potamopyrgus antipodarum* (Gray 1843) appartenant aux hydrobiidés et qui est originaire de la Nouvelle-Zélande a été retrouvé dans le lac Ontario, à 1 km au large de Wilson, New York. Il s'agissait de la première observation de cet escargot dans l'est de l'Amérique du Nord. La densité de *P. antipodarum* a augmenté depuis cette première observation et on s'attend que cet organisme se répande rapidement dans toute la région des Grands Lacs. Le potentiel de *P. antipodarum* comme agent d'encrassement biologique est probablement faible; cependant, la menace la plus sérieuse qu'il laisse planer est la compétition avec les mollusques indigènes pour s'approprier des ressources disponibles. Cette espèce a probablement été introduite dans les eaux de ballast de navires transocéaniques et elle devient le 140^e organisme à être inscrit sur la liste des organismes aquatiques non indigènes introduits dans les Grands Lacs depuis les années 1800. Le risque d'invasion des Grands Lacs par d'autres espèces continue d'exister en dépit des règlements maintenant obligatoires régissant les eaux de ballast.

[Traduit par la Rédaction]

Introduction

The hydrobiid snail *Potamopyrgus antipodarum* (Gray 1843) is native to New Zealand, but is widespread throughout eastern Australia (Ponder 1988) and Europe where it was formerly known as *Potamopyrgus jenkinsi* (Smith 1889) (Winterbourn 1972; Ponder 1988). Initially introduced into Europe from Australasia (Winterbourn 1970), it was first reported from the Thames Estuary, England, in 1859 and in 40 years had spread throughout England and Wales (Hubendick 1950). It was reported on the European mainland in 1899 and by 1920 had spread to many parts of Europe (Adam 1942; Berner 1963). *Potamopyrgus antipodarum* is now widespread throughout Britain (Wallace 1985), Denmark (Lassen 1975), and Switzerland (Ribi 1986) and has most recently been reported from Slovakia (Čejka 1994).

In 1987, *P. antipodarum* was recorded for the first time in North America from the Snake River system in Idaho². The snail was mainly present on filamentous green algae and attached aquatic macrophytes but was also observed occupying rocky boulder habitats (Bowler 1991). By 1989, *P. antipodarum* was the most dominant species of mollusc in all habitats of the Middle Snake River (Bowler 1991) and had spread to Box Canyon Creek, a tributary of the Snake River (Langstein and Bowler 1991). Over the last 10 years, the species has expanded its range from a single locality to over 640 km along the Snake River and its tributaries and has recently crossed the North American continental divide, spreading into the Madison River in the neighbouring Missouri River drainage basin (Bowler and Frest 1996).

Its time and source of introduction are unknown, but it is speculated that the snail was inadvertently introduced from the commercial movement of aquaculture products such as trout eggs and live fish some time during the 1980s (Bowler 1991; Bowler and Frest 1992). Potential threats to native species include domination of preferred habitat, physical covering of egg sites and egg masses, harbouring and support of molluscivorous predators, and attraction of fish predators (Bowler 1991). Crowding owing to immense population densities of *P. antipodarum* (40 000 individuals/m²)

Received March 14, 1996. Accepted September 27, 1996.
J13353

D.T. Zaranko.¹ Zaranko Environmental Assessment Services, 454 College Avenue, Guelph, ON N1G 1T4, Canada.

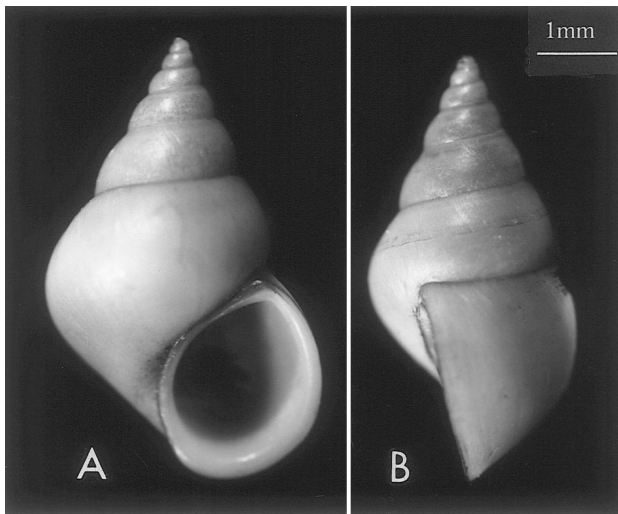
D.G. Farara. Beak Consultants International Inc., 14 Abacus Road, Brampton, ON L6T 5B7, Canada.

F.G. Thompson. Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, U.S.A.

¹ Author to whom all correspondence should be addressed.
e-mail: dzaranko@uoguelph.ca

² Taylor, D.W. 1987. Thousand Islands Preserve threatened and endangered snails. Unpublished report to the Nature Conservancy of Idaho.

Fig. 1. *Potamopyrgus antipodarum*: (A) smooth shell, (B) keeled.



(T.J. Frest, Deixis Consultants, Seattle, Wash., personal communication) is suspected to cause resource competition with native taxa.

Both active and passive dispersal methods have contributed to the spread of *P. antipodarum*. The snail is well suited to passive dispersal by birds (Boycott 1936; Lassen 1975) and has been reported to have passed alive through the alimentary canal of several fish species (Bondesen and Kaiser 1949; Haynes et al. 1985). Large numbers of individuals have been observed floating with *Cladophora* (Ribi and Arter 1986), and among young individuals, floating is common even without a floating substrate (Vareille-Morel 1983). *Potamopyrgus antipodarum* has also been shown to be positively rheotactic (Haynes et al. 1985), moving as much as 60 m upstream in 3 months (Adam 1942).

Potamopyrgus antipodarum inhabits both fresh and brackish water and has been found in water of up to 26‰ salinity (Winterbourn 1970), but it may tolerate higher salinities for a short period of time, as shown in laboratory experiments where it survived a 7-day exposure at 30‰ salinity (Hylleberg and Siegismund 1987). It can successfully exploit both eutrophic and nonpolluted waters (Dorgelo 1988) but is restricted to permanent waterbodies because it lacks resistant stages capable of carrying it over long dry seasons. However, the snail can withstand temporary desiccation, as observed in the Snake River during peak drawdown events of hydroelectric dams (Bowler 1991). It cannot withstand freezing and is limited to water temperatures above 0°C at all salinities (Hylleberg and Siegismund 1987). It is a detritivore–herbivore (Calow and Calow 1975) and prefers to feed on plant and animal detritus but will readily graze on green algae and diatoms (Haynes and Taylor 1984).

The species is readily identified (Fig. 1) by its shell, which is dextral, solid, but not thick walled. The aperture is broadly elliptical in shape with a concave columellar margin. The peristome is complete across the parietal wall. The outer and basal lips are thickened internally. The adult shell has seven to eight whorls and can be up to 12 mm long. The length of the spire is greater than the height of the aperture. The spire is attenuate and concave in profile. The first whorl is minute and raised. The remaining whorls of the spire are evenly rounded between the deeply impressed suture. The body whorl is bluntly angulate

and slightly flattened above the periphery, rounded in occasional specimens. A raised periostracal spiral line and frills may be present. The umbilicus is narrowly perforate. The operculum is ovate in shape, thin, corneas, and paucispiral (the nucleus is below and to the side of the centre); the inner surface has a thin calcareous deposit. These shell features separate this species from all other freshwater snails in North America. The attenuate concave spire with the small protruding apical whorl is unique to this species.

Similar sculpture occurs in the viviparous genus *Pyrgophorus*, which caused that genus to be placed in the synonymy of *Potamopyrgus* for many years. However, species of *Pyrgophorus* are much smaller, they have five or fewer whorls that have a shallower suture, the first embryonic whorl is rounded, and the adult snails are dioecious (Thompson 1968). *Pyrgophorus* occurs in the Gulf of Mexico coastal region of southern North America to northern South America. No species of *Pyrgophorus* in temperate North America resembles *P. antipodarum* in shell characteristics.

In this paper, we document the introduction of *P. antipodarum* into the Great Lakes, describe its known distribution there, and discuss its ecological significance. The specimens upon which this study is based were identified by co-author F.G. Thompson, and voucher specimens (UF260032, UF260033) are deposited in the Museum of Natural History in Gainesville, Florida.

Results and discussion

Potamopyrgus antipodarum was first discovered in Lake Ontario offshore Wilson, New York, in 1991 (Table 1; Fig. 2). No individuals were collected from this station location in 1990. In successive years, densities at this station fluctuated from year to year and varied seasonally (Table 1). Mean densities were highest in the fall compared with the spring. Highest mean densities were noted in October 1995, reaching 5653 individuals/m².

Potamopyrgus antipodarum has a high reproductive capacity in that it is ovoviviparous or populations may be entirely parthenogenic, with varying proportions of sexually functional males. Males usually make up less than 5% of the total population (Wallace 1985). Of the specimens examined from Lake Ontario, only females have been noted. Because of its parthenogenic nature, the relocation of one individual could give rise to a new population.

Reproductive output has been linked to water temperature, with the highest number of young produced in the summer (Frenzel 1979). *Potamopyrgus antipodarum* has an annual life cycle and reaches sexual maturity at approximately 3.5 mm and can produce an average of 230 juveniles per year (Lassen 1979). Live specimens from Lake Ontario that were maintained in aquariums for 2 months at 21°C produced 9.6 young per adult each month, ranging in size from 0.39 to 1.59 mm (R. Dermott, Department of Fisheries and Oceans, Burlington, Ont., personal communication). The reproductive success of *P. antipodarum* is shown in Table 1; densities are much higher in the fall compared with the spring. However, a large proportion of the individuals in the fall were young snails (i.e., <2 mm) and appear to have not survived through the winter. Mortality rate varies with age and is the highest during the first 2 months of life (65–99%) (Frenzel 1979).

Table 1. Mean densities (number/m²) of *P. antipodarum* in Lake Ontario.

Location	Date	Latitude	Longitude	Mean density (SD)	
Port Dalhousie (stn. 1)	May 1994	43°13'27"	79°17'03"	23 (32)	
	August 1994			46 (48)	
Port Weller (stn. 2)	August 1994	Inner harbour	43°14'44"	79°12'55"	13 (22) ^a
		Midchannel	43°14'14"	79°12'58"	327 (138) ^b
		Entrance	43°14'36"	79°13'02"	45 (30)
		Nearshore north	43°15'14"	79°12'33"	77 (58)
		Six Mile Creek (stn. 3)	May 1994	43°19'12"	78°58'45"
Offshore Wilson, N.Y. (stn. 4)	August 1994			77 (27)	
	July 1990	43°19'36"	78°52'06"	0	
	April 1991			282 (164)	
	October 1991			1301 (960)	
	April 1992			0	
	October 1992			160 (137)	
	April 1993			70 (73)	
	October 1993			760 (874)	
	April 1994			77 (133)	
	October 1994			293 (187) ^b	
	April 1995			244 (188)	
	October 1995			5653 (1142)	
Offshore Kingston (stn. 5)	August 1994	44°12'51"	76°31'19"	109 (40)	
North Channel (stn. 6) (offshore Amherst Island)	April 1994	44°10'53"	76°44'08"	154 (90)	
	August 1994			104 (44)	
Prescott (stn. 7)	April 1994	44°41'54"	75°31'53"	15 (34)	

Note: Specimens were collected with a 600- μ m sieve except those at Station 4 which were collected with a 200- μ m sieve.

^aAll these individuals were keeled.

^bApproximately 95% of these individuals were keeled; all other specimens from all stations were smooth-shelled.

A similar seasonal pattern for *P. antipodarum* was found in Lake Alexandrina, New Zealand, where abundance peaked in late summer or autumn and lowest numbers were observed in early spring (Talbot and Ward 1987).

Across Lake Ontario, *P. antipodarum* was found in 7 of 26 locations sampled in 1994 (Fig. 2). During this year, the largest populations of *P. antipodarum* were found offshore Wilson, New York (station 4), and Port Weller (station 2) midchannel (293 and 327 individuals/m², respectively) (Table 1).

Most of the collected *P. antipodarum* had no periostracal ornamentation (i.e., keel) (Fig. 1A), but over 95% of the individuals at two stations in Port Weller (station 2) and offshore Wilson, New York (station 4, October 1994) were keeled (Fig. 1B). The average height of collected individuals (600- μ m screen) was between 5 and 6 mm (excluding individual collected at station 4; 200- μ m screen). The highly variable shell size, shape, and ornamentation may be the result of exposure to different environmental conditions (Dell 1953; Hunter 1961). However, Winterbourn (1970) has pointed out that environmental influence is not the only factor governing shell ornamentation and suggested that there must be a genetic basis.

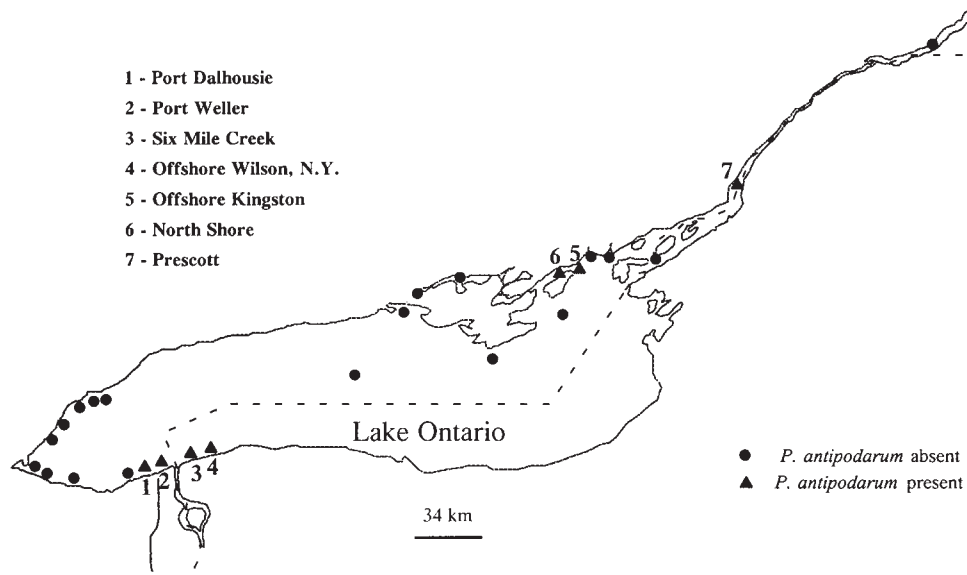
The snail was collected from water depths ranging between 4 and 25 m. *Potamopyrgus antipodarum* were found in sediments that were generally a silty sand. The particle size of the sediments at the stations was similar, with a large percentage of the particles being less than 63 μ m (Table 2).

To date, *P. antipodarum* has not been collected from

surveyed stations in Lake Erie or Lake Huron. In Lake Erie, 16 stations were surveyed in the western basin in 1991 from the Maumee River around to Point Pelee (Farara and Burt 1993). In the summer of 1992, 47 stations were surveyed in Lake Erie (Farara 1995), and from May 1993 to October 1993, two stations in each basin of the lake were surveyed monthly (Fig. 3) (Dahl et al. 1995). In Lake Huron, five stations were surveyed in 1995 (South Bay, Stokes Bay, Port Elgin, Goderich, and Cape Ipperwash) (MOEE 1995, unpublished data from the Great Lakes Surveillance Project).

Ballast water discharged from transoceanic vessels has been the implicated mode by which many exotics have been introduced into the Great Lakes (Mills et al. 1993). To date, introduced exotic species number 139 organisms. Not included in this total is the meiobenthic freshwater tubificid *Gianius aquaedulcis*, previously only known from Europe and discovered in the Niagara River in 1983 (Farara and Erséus 1991). Almost one third of this total has been introduced in the last 30 yr, coinciding with the opening of the St. Lawrence Seaway in 1959 (Mills et al. 1993). Molluscs make up approximately 10% of these introduced species and include the zebra mussel *Dreissena polymorpha* (Hebert et al. 1989), the quagga mussel *Dreissena bugensis* (May and Marsden 1992), the faucet snail *Bithynia tentaculata*, and sphaeriid clams (*Sphaerium corneum* and *Pisidium amnicum*) (Mills et al. 1993).

Twenty-nine percent of all exotic species introductions into the Great Lakes are linked to shipping activities of which ballast water discharge is the main vehicle of distribution (Mills

Fig. 2. Distribution of *P. antipodarum* in Lake Ontario.**Table 2.** Sediment characteristics at stations supporting populations of *P. antipodarum*.

Location	Water depth (m)	Sand, 63–1000 μm (%)	Fines, <63 μm (%)	Organic content
Port Dalhousie (stn. 1)	18.5	35.9	64.1	6.2 mg TOC/g
Port Weller (stn. 2)				
Inner harbour	4.8	8.9	91.1	69.8
Midchannel	9.3	8.4	91.6	
Entrance	9.4	69.1	30.9	
Nearshore	13.9	30.2	69.8	
Six Mile Creek (stn. 3)	17.8	30.0	70.0	
Offshore Wilson, N.Y. (stn. 4)	15–20	80.6 ^a	19.4	1.13–1.36% (LOI)
Offshore Kingston (stn. 5)	11.6	69.9	30.1	
North Channel (stn. 6)	24.2	16.2	83.8	69.9 mg TOC/g
Prescott (stn. 7)	4.0	39.3	60.7	23 mg TOC/g

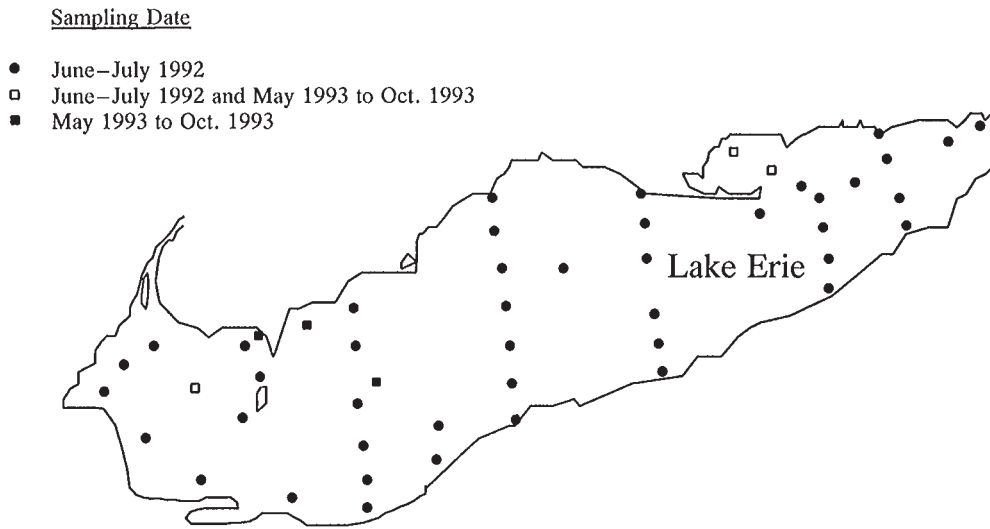
^aThe bulk of the sediment at this station was <250 μm .

et al. 1993). Both localities of Lake Ontario where *P. antipodarum* inhabit are in areas near heavy ship traffic (the Welland Canal and the North Channel). The present known distribution of *P. antipodarum* may be a result of separate introductions, but data are not available from the southern shoreline of Lake Ontario to substantiate this observation. Ballast water discharge from cargo boats was the suspected vehicle by which *P. antipodarum* was recently introduced into parts of Europe (Čejka 1994) and is suspect, once again, in the introduction of *P. antipodarum* into the Great Lakes ecosystem.

The survival of *P. antipodarum* in the ballast water of a ship is probable because of its high tolerance of saline conditions (Hylleberg and Siegismund 1987). In studying the effectiveness of ballast water exchange, Locke et al. (1993) noted that approximately 50% of surveyed vessels that exchanged ballast water midocean reached final salinities of $\geq 30\text{‰}$. Consequently, *P. antipodarum* could easily survive an oceanic crossing in a vessel that had incomplete ballast water exchange. To stop the invasion of saline-tolerant freshwater exotics, ballast water exchange must be complete and final salinities must meet or exceed the 30‰ salinity level of U.S. Ballast Water Management regulations (U.S. Coast Guard 1993).

Although the snail is of New Zealand origin, it is not known where the populations in Lake Ontario originated from, as it is now widespread throughout Europe. Once introduced, *P. antipodarum* spreads quickly in aquatic environments. In the Kysing Fjord, Denmark, it recolonized 2 km of an estuary in 6 months (Siegismund and Hylleberg 1987). Densities peaked at 50 000 individuals/m² in summer months but subsequently crashed to nearly zero in winter when the estuary froze (Siegismund and Hylleberg 1987). In Lake Zürich, Switzerland, *P. antipodarum* extended its range over more than 20 km from the location where it was first discovered in less than 10 years (Ribi 1986). Densities were reported to have peaked at 100 000 individuals/m² but dropped two orders of magnitude in subsequent years (Ribi and Arter 1986).

In the Snake River system, *P. antipodarum* is now broadly distributed with highly variable densities. Populations are large in the mainstem of the Snake River (16 000–40 000/m²) (T.J. Frest, personal communication), making up greater than 85% of the snails present (Bowler 1991). Highest densities (up to 40 000/m²) (T.J. Frest, personal communication) were noted in impoundment habitats (Bowler 1991) and below fish hatcheries and lower densities (600–6000/m²) (T.J. Frest, personal

Fig. 3. Locations in Lake Erie where *P. antipodarum* was not found in 1992 and 1993.

communication) in springs above pollution sources (Frest and Bowler 1993).

In New Zealand, *P. antipodarum* has been recorded from lowland rivers, stony streams, creeks, ponds, lakes, springs, and estuaries. It has been found in waters with high and low calcium content, on hard and soft substrates, and amongst vegetation (Winterbourn 1970). It is usually dominant or subdominant in both the littoral and profundal areas of most New Zealand lakes (Talbot and Ward 1987). In 1994, *P. antipodarum* was recorded in two localities from the Slovak section of the Dunaj River (Čejka 1994) in areas lacking macrophytes with pebble and rocky bottoms. However, as their name suggests (i.e., mud snails), most inhabit sediments that are typically a silty sand which was the preferred habitat for populations in Lake Ontario.

Because of the snail's ability to tolerate a wide variety of habitats and environmental conditions, its high reproductive capacity, and the variety of dispersal methods once the species is present in a waterbody, *P. antipodarum* will probably spread quickly throughout the Great Lakes area as it has in Europe, southeastern Australia, and Tasmania. In Lake Ontario, densities of *P. antipodarum* appear to be increasing since its discovery in 1991, but are far short of the maximums observed in Europe and the Snake River system. Its spread may be limited to water depths less than 25 m in lentic environments, but its ubiquitous nature will probably make it very successful in lotic environments. The biofouling potential of *P. antipodarum* is probably low compared with that of the zebra mussel, but the snails have been known to breed in freshwater tanks and reservoirs and pass through water pipes to emerge from domestic taps (Ponder 1988) as well as block waterpipes and meters (Cotton 1942). However, its most serious threat may be competition with native molluscs in that crowding owing to immense population densities, a result of its parthenogenic nature, may cause resource competition such as domination of preferred habitat.

Acknowledgements

The authors thank Ronald Dermott, Department of Fisheries

and Oceans (DFO), and Todd Howell, Ontario Ministry of Environment and Energy (OMOEE) and Ecological Services for Planning, Guelph, Ont., for provision of benthic and supporting data. Data provided by OMOEE were from the Great Lakes Embayments and Harbours Investigation Program (GLEAHIP) and the Great Lakes Surveillance Project. Data provided by DFO were from the Lake Ontario Bioindex Project, Lake Erie Trophic Transfer Project, and Lake Erie Bio-monitor Project. Extended thanks go to Robert Herschler, Smithsonian Institute, Washington, D.C., who verified the identifications. Kurt Auffenberg, Florida Museum of Natural History, assisted with the preparation of the photographs. Extended thanks to Gerald L. Mackie, University of Guelph, for helping with the initial identifications and Terrence J. Frest for providing information on *P. antipodarum* in the Snake River system.

References

- Adam, W. 1942. Sur la répartition et la biologie de *Hydrobia jenkinsi* (Smith) en Belgique. Bull. Mus. R. Hist. Nat. Belgique, **18**: 1–18.
- Berner, L. 1963. Sur d'invasion de la France par *Potamopyrgus jenkinsi* (Smith). Arch. Molluskenkd. **92**: 19–29.
- Bondesen, P. and Kaiser, E.W. 1949. *Hydrobia (Potamopyrgus) jenkinsi* (Smith) in Denmark illustrated by its ecology. Oikos, **1**: 252–281.
- Bowler, P. 1991. The rapid spread of the freshwater hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the middle Snake River, southern Idaho. Proc. Desert Fish. Council. **21**: 173–182.
- Bowler, P.A., and Frest, T.J. 1992. The non-native snail fauna of the Middle Snake River, Southern Idaho. Proc. Desert Fish. Council. **23**: 28–44.
- Bowler, P.A., and Frest, T.J. 1996. The advancing distribution of the New Zealand mud snail, *Potamopyrgus antipodarum* (Gray), in North America. Contributed paper. Am. Malacol. Union, 62nd Annual Meeting, Chicago, Ill.
- Boycott, A.E. 1936. The habits of fresh water molluscs in Britain. J. Anim. Ecol. **5**: 116–186.
- Calow, P., and Calow, L.J. 1975. Cellulase activity and niche separation in freshwater gastropods. Nature (Lond.), **255**: 478–480.
- Čejka, T. 1994. First record of the New Zealand mollusc *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae) from

- the Slovak section of the Dunaj River. Biol. Bratislava, **49**: 657–658.
- Cotton, B.C. 1942. Some Australian freshwater Gastropoda. Trans. R. Soc. S. Aust. **66**: 75–82.
- Dahl, J.A., Graham, D.M., Dermott, R., Johannsson, O.E., Millard, E.S., and Myles, D.D. 1995. Lake Erie 1993, western, west central and eastern basins: change in trophic status, and assessment of the abundance, biomass and production of the lower trophic levels. Can. Tech. Rep. Fish. Aquat. Sci. No. 2070.
- Dell, R.K. 1953. The freshwater Mollusca of New Zealand, Part 1. The genus *Hydriddella*. Trans. R. Soc. N.Z. **81**: 221–237.
- Dorgelo, J. 1988. Growth in a freshwater snail under laboratory conditions in relation to eutrophication. Hydrobiologia, **157**: 125–128.
- Farara, D.G. 1995. Benthic meio-macroinvertebrates present in samples collected for the Lake Erie Trophic Transfer (LETT) project: 1992. Report prepared for Ron Dermott, Department of Fisheries and Oceans, Great Lakes Laboratory, Burlington, Ont., by Beak Consultants Limited, Brampton, Ont.
- Farara, D.G., and Burt, A.J. 1993. Environmental assessment of western Lake Erie sediments and benthic communities: 1991. Report prepared for the Ontario Ministry of Environment and Energy, Water Resources Branch, Great Lakes Section, by Beak Consultants Limited, Brampton, Ont.
- Farara, D.G., and Erséus, C. 1991. *Phalodrilus aquaedulcis* (Hrab 1960), a meiobenthic freshwater oligochaete (Tubificidae) previously known only from Europe, recorded from the Niagara River, North America. Can. J. Zool. **69**: 291–294.
- Frenzel, P. 1979. Untersuchungen zur Biologie und populations dynamik von *Potamopyrgus jenkinsi* (Smith) (Gastropoda: Prosobranchia) im Litoral des Bodensees. Arch. Hydrobiol. **85**: 448–464.
- Frest, T.J., and Bowler, P.A. 1993. A preliminary checklist of the aquatic and terrestrial molluscs of the Middle and Snake River sub-basin. Proc. Desert Fish. Council. **24**: 53–58.
- Gray, J.E. 1843. Catalogue of the species of Mollusca and their shells, which have hitherto been recorded as found at New Zealand, with the description of some lately discovered species. Travels N.Z. **2**: 228–265.
- Haynes, A., and Taylor, B.J.R. 1984. Food finding and food preference in *Potamopyrgus jenkinsi* (Smith E.A.) (Gastropoda: Prosobranchia). Arch. Hydrobiol. **100**: 479–491.
- Haynes, A., Taylor, B.J.R., and Varley, M.E. 1985. The influence of the mobility of *Potamopyrgus jenkinsi* (Smith, E.A.) (Prosobranchia:Hydrobiidae) on its spread. Arch. Hydrobiol. **103**: 497–508.
- Hebert, P.D.N., Muncaster, B.W., and Mackie, G.L. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. **46**: 1587–1591.
- Hubendick, B. 1950. The effectiveness of passive dispersal in *Hydrobia jenkinsi*. Zool. Bidr. Upps. **28**: 493–504.
- Hunter, W.R. 1961. Life cycles of four freshwater snails in limited populations in Loch Lomond with a discussion of infraspecific variation. Proc. Zool. Soc. Lond. **137**: 135–171.
- Hylleberg, J., and Siegismund, H.R. 1987. Niche overlap in mud snails (Hydrobiidae): freezing tolerance. Mar. Biol. (Berlin), **94**: 403–407.
- Langstein, S., and Bowler, P. 1991. On-going macroinvertebrate analysis using the Biotic Condition Index and the appearance of *Potamopyrgus antipodarum* (Gray) in Box Canyon Creek, southern Idaho. Proc. Desert Fish. Council. **21**: 183–194.
- Lassen, H.H. 1975. The migration potential of freshwater snails exemplified by the dispersal of *Potamopyrgus jenkinsi*. Nat. Jutl. **20**: 237–242.
- Lassen, H.H. 1979. Reproductive effort in Danish mudsnails (Hydrobiidae). Oecologia, **40**: 365–369.
- Locke, A., Reid, D.M., vanLeeuwen, H.C., Sprules, W.G., and Carlton, J.T. 1993. Ballast water exchange as a means of controlling dispersal of freshwater organisms by ships. Can. J. Fish. Aquat. Sci. **50**: 2086–2093.
- May, B., and Marsden, J.E. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. Can. J. Fish. Aquat. Sci. **49**: 1501–1506.
- Mills, E.L., Leach, J.G., Carlton, J.T., and Secor, C.I. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. **19**: 1–54.
- Ponder, W.F. 1988. *Potamopyrgus antipodarum*, a molluscan colonizer of Europe and Australia. J. Molluscan Stud. **4**: 271–286.
- Ribi, G. 1986. Within-lake dispersal of the prosobranch snails, *Viviparus ater* and *Potamopyrgus jenkinsi*. Oecologia, **69**: 60–63.
- Ribi, G., and Arter, H. 1986. Colonization of Lake Zürich by the prosobranch snail *Potamopyrgus jenkinsi* between 1980 and 1984. Vierteljahrsschr. Naturforsch. Ges. Züer. **131**: 52–57.
- Siegismund, H.R., and Hylleberg, J. 1987. Dispersal-mediated coexistence of mud snails (Hydrobiidae) in an estuary. Mar. Biol. (Berlin), **94**: 39–402.
- Smith, E.A. 1889. Notes on British Hydrobiae with a description of a supposed new species. J. Conchol. **6**: 142–145.
- Talbot, J.M., and Ward, J.C. 1987. Macroinvertebrates associated with aquatic macrophytes in Lake Alexandrina, New Zealand. N.Z. J. Mar. Freshwater Res. **21**: 199–213.
- Thompson, F.G. 1968. The aquatic snails of the family Hydrobiidae of Peninsular Florida. University of Florida Press, Gainesville, Fla.
- U.S. Coast Guard. 1993. Ballast water management for vessels entering the Great Lakes 33-CFR Part 151.1510. Effective date May 10, 1993. U.S. Coast Guard.
- Vareille-Morel, C. 1983. Les mouvements journaliers du mollusque *Potamopyrgus jenkinsi* Smith. Étude sur le terrain et en laboratoire. Haliotis, **13**: 31–34.
- Wallace, C. 1985. On the distribution of the sexes of *Potamopyrgus jenkinsi* (Smith). J. Molluscan Stud. **51**: 290–296.
- Winterbourn, M. 1970. The New Zealand species of *Potamopyrgus* (Gastropoda: Hydrobiidae). Malacologia, **10**: 283–321.
- Winterbourn, M.J. 1972. Morphological variation of *Potamopyrgus jenkinsi* (Smith) from England and a comparison with the New Zealand species, *Potamopyrgus antipodarum* (Gray). Proc. Malacol. Soc. Lond. **40**: 133–145.