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Lake Superior: an invasion coldspot?

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Abstract

Lake Superior receives a disproportionate number of ballast water discharges from transoceanic ships operating on the Laurentian Great Lakes. Although this provides dispersal opportunities for nonindigenous species (NIS), relatively few NIS were initially discovered in this lake prior to being recorded elsewhere in the basin. A lack of NIS records from this lake may be an artefact of sampling bias. We tested this hypothesis by sampling benthos and plankton from littoral and deepwater habitats around the perimeter of Lake Superior during June and August 2001. Using morphological analysis techniques, we identified a total of 230 invertebrate taxa representing planktonic, benthic and nektonic lifestyles. Five species with invasion histories in the lower Great Lakes, the bivalves *Sphaerium corneum*, *Pisidium amnicum* and *P. moitessierianum*, gastropod *Potamopyrgus antipodarum* and amphipod *Echinogammarus ischnus*, were identified for the first time in Lake Superior. In addition, records of expanded distributions within this lake are presented for the amphipod *Gammarus fasciatus* and oligochaetes *Ripistes parasita* and *Vejdovskyella intermedia*. Recently introduced NIS in Lake Superior were found near international ports, implicating shipping as the vector of their introduction. Intrinsic physical-chemical aspects of Lake Superior may account for the scarcity of NIS in this lake as compared to the lower Great Lakes.

Introduction

Since European colonization, human activity has facilitated the introduction of nonindigenous species (NIS) into the Laurentian Great Lakes region (Mills et al., 1993; Ricciardi & MacIsaac, 2000). Some 99 new species of aquatic animals and protists have become established in the Great Lakes and their drainage basins since the early 1800s (Fig. 1). Ballast water discharge from commercial ships has been the primary mechanism for these introductions (Mills et al., 1993; Ricciardi, 2001). Since 1959, more than 90% of transoceanic vessels entered the Great Lakes with cargo and thus had "no ballast on board" (NOBOB) status (Colautti et al., 2003; Grigorovich et al., 2003). Ballast water management regulations (Canada, 1989; U.S.A., 1993) require vessels officially laden with ballast water to undergo open-ocean exchange. NOBOB vessels are not subject to these regulations even though they carry residual ballast water and associated biota (Aquatic Sciences, 1996; Bailey et al., 2003). After unloading freight at Great Lakes' ports, NOBOB ships typically fill their ballast tanks with Great Lakes' water to compensate for loss of cargo weight. As a result, residual ballast water and sediment get mixed with Great Lakes' water in ballast tanks of NOBOB ships. During 1981–2000, ~70% of NOBOB vessels made their final stop at Lake Superior, where they discharged the mixed ballast as new cargo was loaded; in addition, this lake received ~75% of ballast water discharges from transoceanic ballasted ships navigating the lakes (Grigorovich et al., 2003). Such

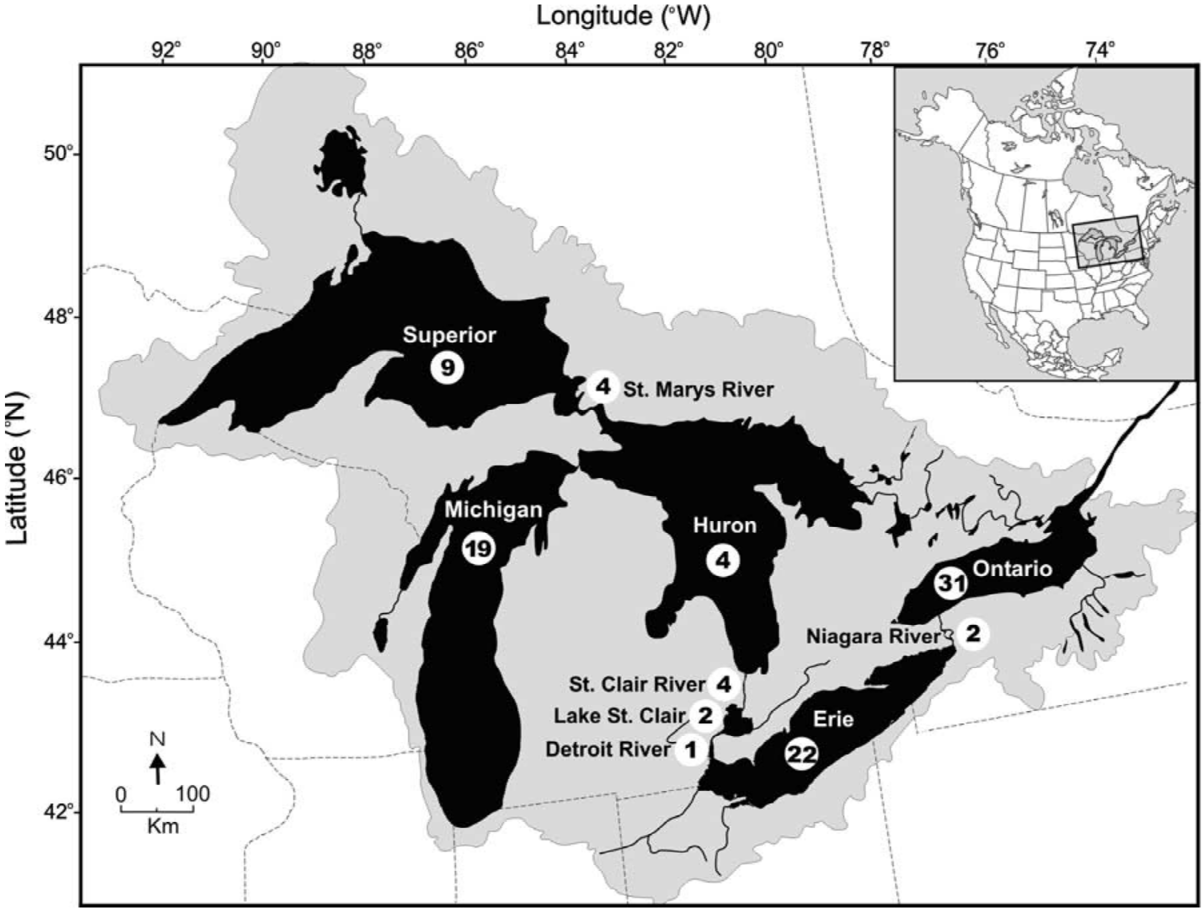

Figure 1. Map of the Laurentian Great Lakes basin (shaded) showing number of sites of first discovery for established nonindigenous aquatic animals and protists by open-water location. Sites in surrounding drainage systems are ascribed to immediate downstream open-water locations.

disproportionate deballasting activities could facilitate the introduction of NIS into Lake Superior.

Since the early 1800s, only nine nonindigenous animal and protist species new to the Great Lakes basin were initially recorded in Lake Superior, including eight NIS discovered after 1959 when the St. Lawrence Seaway was completed (Pronin et al., 1998; reviewed in Grigorovich et al., 2003). Although a number of possibilities exist that may explain the under-representation of Lake Superior as a site of initial discovery of Great Lakes' NIS, this pattern may specifically reflect inadequate sampling effort compared to the lower Great Lakes.

In this study, we survey littoral and deepwater habitats around the perimeter of Lake Superior to determine if sampling bias accounted for the lack of first records of NIS in this lake. We describe the first records in Lake Superior for five NIS with prior invasion histories in the lower Great Lakes – the Eurasian bivalves *Sphaerium corneum*, *Pisidium amnicum* and *P. moitessierianum*, New Zealand gastropod *Potamopyrgus antipodarum* and Ponto-Caspian amphipod *Echinogammarus ischnus*. Further, we document expanded ranges for two other NIS already resident in the lake – the Atlantic amphipod *Gammarus fasciatus* and Eurasian oligochaete *Ripistes parasita*. In addition, we provide the first record of the Holarctic oligochaete *Vejdovskyella intermedia* from Lake Superior and St. Marys River and assess its morphological characteristics. We also describe an anomalous form of *Vejdovskyella*, which is morphologically intermediate between *V. intermedia* and Eurasian *V.* cf. *macrochaeta*; its appearance in Lake Superior raises the possibility of an intercontinental introduction from Europe. We report no NIS new to the Great Lakes basin and examine hypotheses that may account for the relative rarity of NIS in this lake.

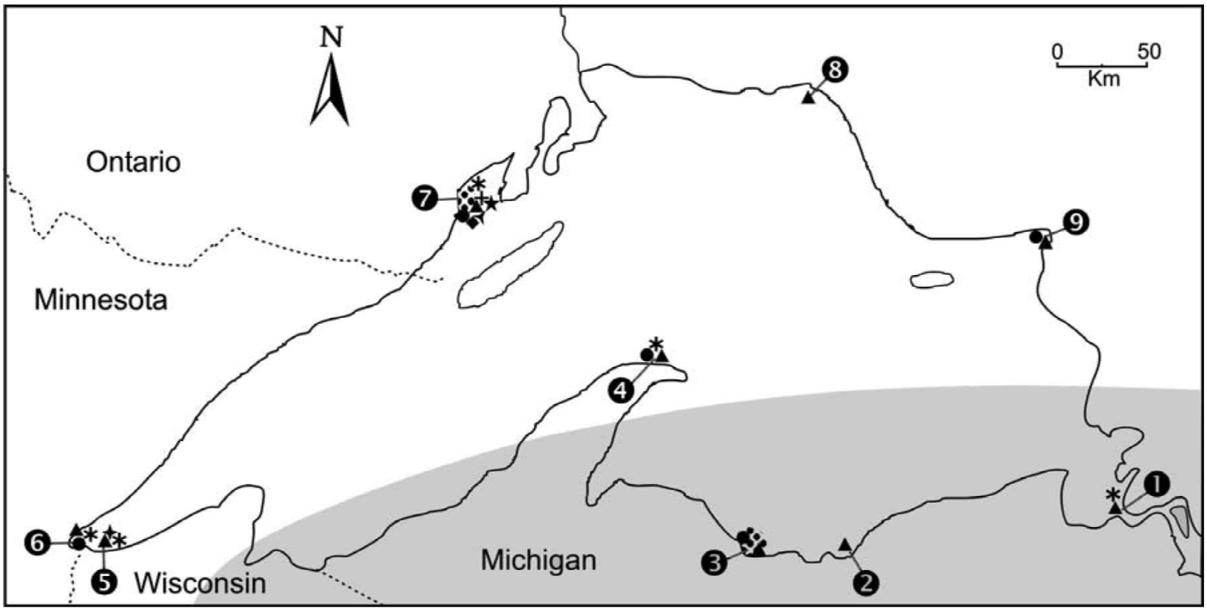

Figure 2. Map of Lake Superior showing sampling areas: 1 – Sault Ste. Marie; 2 – Munising; 3 – Marquette; 4 – Copper Harbor; 5 – Superior; 6 – Duluth; 7 – Thunder Bay; 8 – Marathon; and 9 - Wawa (Michipicoten Bay). Sites of occurrences of *Gammarus fasciatus* (▲), *Vejdovskyella intermedia* (∗), *Ripistes parasita* (•), *Sphaerium corneum* (⋆), *Pisidium amnicum* (⤙), *Pisidium moitessierianum* (✚), *Potamopyrgus antipodarum* (⧫) and *Echinogammarus ischnus* (+). Previously reported distribution of *Gammarus fasciatus* (▒) and *Ripistes parasita* (⁙).

Methods

During June and August 2001, zooplankton and zoobenthos samples were collected from littoral near-shore (within <200 m from shoreline) and deepwater offshore (>1 km) sites in Lake Superior. Sampling was conducted at nine areas around the perimeter of the lake (Fig. 2). Two locations were surveyed near Duluth and Thunder Bay harbours to increase the likelihood of detecting NIS, as these two ports receive a disproportionate number of visits by transoceanic ballasted and NOBOB vessels (Colautti, 2001). At near-shore sites, depths ranged from 3.4 to 19.2 m (mean = 7.0; SD = 3.5); benthos was sampled using a combination of sled dredge (inlet 0.38 m, mesh 250 μm) and ponar grab (area 225 cm^{-2}). Most of the near-shore zone was underlain with bedrock and coarse-textured till consisting of sand, gravel, pebbles and boulders; this substrate was overlain with fine-grained sediments including mud, silt and detritus of plant origin. At offshore sites, depths ranged from 7.4 to 64.2 m (mean = 25.1; SD = 14.2); samples were collected with a ponar grab; mud, silt and clay were the predominant sediments. Ponar samples were washed through sieves with either 125 or 500 μm mesh sizes. Zooplankton was sampled by vertical hauls using a 0.5 m diameter, 53 μm mesh plankton net. During June 2001, vertical tows 3 – 8 m deep were made at near-shore sites, while tows 7 – 23 m deep were made at offshore sites. The entire water column was sampled during August 2001, when the lake was stratified.

All samples were preserved in 95% ethanol. In the laboratory, macroinvertebrates were separated from other material before identification. Zooplankton and zoobenthos were sorted into general taxonomic categories under a Leica dissecting microscope. Copepods, cladocerans and oligochaetes were dissected and mounted in CMC-9AF mounting media for morphological examination.

In total, 40 zooplankton and 94 zoobenthos samples were examined. Most of the taxa were identified to the lowest taxonomic level feasible. Our benthic analyses focused on the Oligochaeta, Gastropoda, Bivalvia and Amphipoda because these are among the best-studied groups of introduced macroinvertebrates in the Great Lakes (e.g., Mills et al., 1993). Representatives of these groups include easily recognizable invaders owing to their distinctive morphology (e.g., *Ripistes parasita*, *Potamopyrgus antipodarum*,

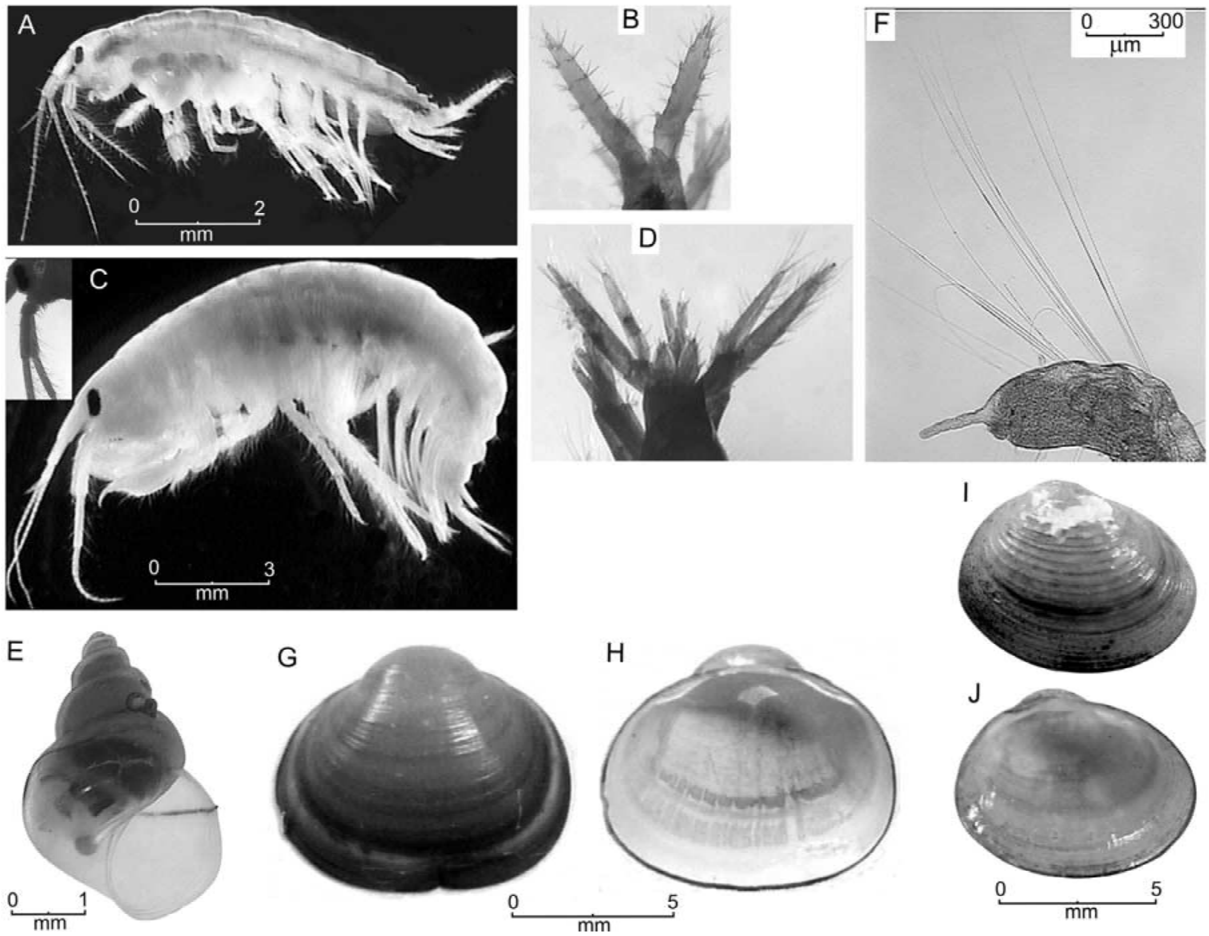

Figure 3. Nonindigenous invertebrates from Lake Superior. Female *Echinogammarus ischnus*: lateral view of body (*A*) and dorsal view of uropods III and telson (*B*); male *Gammarus fasciatus*: lateral view of body (*C*) and dorsal view of uropods III and telson (*D*); note acute upper angle of interantennal lobe of head and straight setae on antennae II (inset); female *Potamopyrgus antipodarum* (*E*); note thin, semi-transparent shell and threadlike peripheral keel on body whorl; *Ripistes parasita* (*F*); *Sphaerium corneum*: outer (*G*) and inner (*H*) surface of valve; and *Pisidium amnicum*: outer (*I*) and inner (*J*) surface of valve.

Echinogammarus ischnus and *Gammarus fasciatus*; Fig. 3). Sphaeriid bivalves are much less differentiated morphologically and as such may remain undetected for an extended time. Images of invertebrates were outputted from Leica DME dissecting and Leica $MZ7_5$ compound microscopes to Optimas 6.2 image analysis software on a personal computer.

We deposited in the Canadian Museum of Nature (CMN) voucher specimens of *G. fasciatus* (preserved in ethanol; catalogue Nos. CMNC 2002-0079 to 0082), *P. antipodarum* (preserved in ethanol; CMNML 093666) and oligochaetes (mounted in cmC-9AF media), including *Ripistes parasita* (CMNA 2002-0009 to 0010), *Vejdovskyella* cf. *macrochaeta* and *V. intermedia* (CMNA 2002-0020 to 0027).

Results and discussion

Species account

We collected representatives of ten invertebrate phyla, namely Porifera, Cnidaria, Platyhelminthes, Rotifera, Nematoda, Bryozoa, Annelida, Arthropoda, Tardigrada, and Mollusca. We identified a total of 230 taxa representing planktonic, benthic and nektonic life styles (see Appendices I and II). Taxa native to the Laurentian Great Lakes, or those Holarctic in distribution, collectively accounted for up to 95% of the total number of specimens identified. However, some taxa were designated to levels insufficient to determine whether they were native or introduced. Nonindigenous invertebrates represented between 5 and 10%

of the taxa recorded at individual locations surveyed (Appendices I and II). Only two nonindigenous pelagic crustaceans, *Bosmina coregoni* and *Bythotrephes longimanus*, were collected, both of which have been previously recorded in this lake (Mills et al., 1993). *Bosmina coregoni* was reported only from Duluth and Superior harbours, whereas *B. longimanus* was widespread throughout the lake. In addition, *Dreissena* veligers were detected in plankton tows collected in Duluth and Superior harbours, indicating the presence of reproducing populations nearby (Kraft et al., 1991). Other planktonic NIS known to occur in Lake Superior (e.g., *Eurytemora affinis*, *Cyclops strenuus*) or the other Great Lakes (e.g., *Skistodiaptomus pallidus*, *Cercopagis pengoi*) were not found in this survey.

During August 2001, settled *Dreissena polymorpha* (individuals 3.2 – 7.0 mm long) were detected in the littoral waters of Thunder Bay and Superior harbours, but were not found in two other areas near Sault Ste. Marie and Marquette, where this species has been observed previously (U.S. Geological Survey, 2002). In Duluth and Superior harbours, densities of zebra mussels ranged from ~0.3 – 130 individuals m^{-2} during the growth season of 1993 (C. Kraft, Cornell University, Ithaca, New York, unpublished data).

Five NIS with prior invasion histories in the lower Great Lakes, the Eurasian bivalves *Sphaerium corneum*, *Pisidium amnicum* and *P. moitessierianum*, New Zealand gastropod *Potamopyrgus antipodarum* and Ponto-Caspian amphipod *Echinogammarus ischnus*, were discovered for the first time from Lake Superior. Populations of *S. corneum* and *P. amnicum* occurred in littoral habitats near Thunder Bay harbour at average densities of 61 and 108 individuals m^{-2}, respectively. *Pisidium moitessierianum* was found at a density of 145 individuals m^{-2} in the Superior harbour. Two individuals of *P. antipodarum*, including one juvenile (2.7 mm long) and one adult female (3.7 mm long), were collected from sandy substrate at a depth of 8.9 m offshore of Thunder Bay. Two individuals of *E. ischnus*, including one juvenile (3.7 mm long) and one egg-carrying female (6.3 mm long; Fig. 3A), were recorded from silty-sand substrate in littoral waters (4.5 m depth) adjacent to Thunder Bay harbour. In addition, we observed the oligochaete *Ripistes parasita* and amphipod *Gammarus fasciatus* beyond their previously reported distributions in Lake Superior. Individuals of the European native *R. parasita* were found at five sampling areas, of which three are new intra-lake distribution records (Table 1; Fig. 2). Populations consisted of non-budding and budding immature specimens (1.6–2.8 mm long). *Ripistes parasita* was collected in vegetated (e.g., *Chara*) and rocky habitats from depths ranging between 5.8 and 7.4 m.

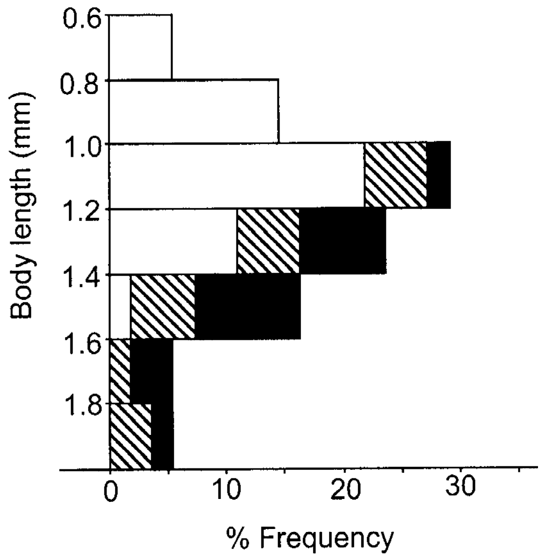

Figure 4. Length frequency distribution of *Vejdovskyella intermedia*; 1 km offshore Duluth, August 2001. Reproductive condition and maturity of individuals (n = 36): single, immature (□); budding, immature (▧); and single, mature (■).

Gammarus fasciatus was collected in six additional locations beyond its previously known distribution in Lake Superior (Table 1; Fig. 2). One to three individuals of *G. fasciatus* were encountered in each ponar sample taken in areas 5–9, while 22 individuals were collected by bottom sled in littoral waters near Copper Harbor (Fig. 2). This population included adult males, ovigerous females and juveniles, and thus was likely self sustaining. At the three sampling locations within its previous range (Holsinger, 1976), populations of *G. fasciatus* occurred at densities up to 150–240 individuals m^{-2}.

We collected several oligochaete species that represent possible introductions from Europe, namely *Stylodrilus heringianus*, *Spirosperma ferox*, *Potamothrix moldaviensis* and *P. vejdovskyi* (Appendix II). In North America, their range is restricted largely to the Great Lakes basin, despite their broad inland distribution in Europe (Cook & Johnson, 1974). All of these species were previously known from Lake Superior (Spencer, 1980).

Three distinctive forms of the oligochaete genus *Vejdovskyella* were found, of which two, *V. comata* and *V. intermedia*, are Holarctic in distribution and

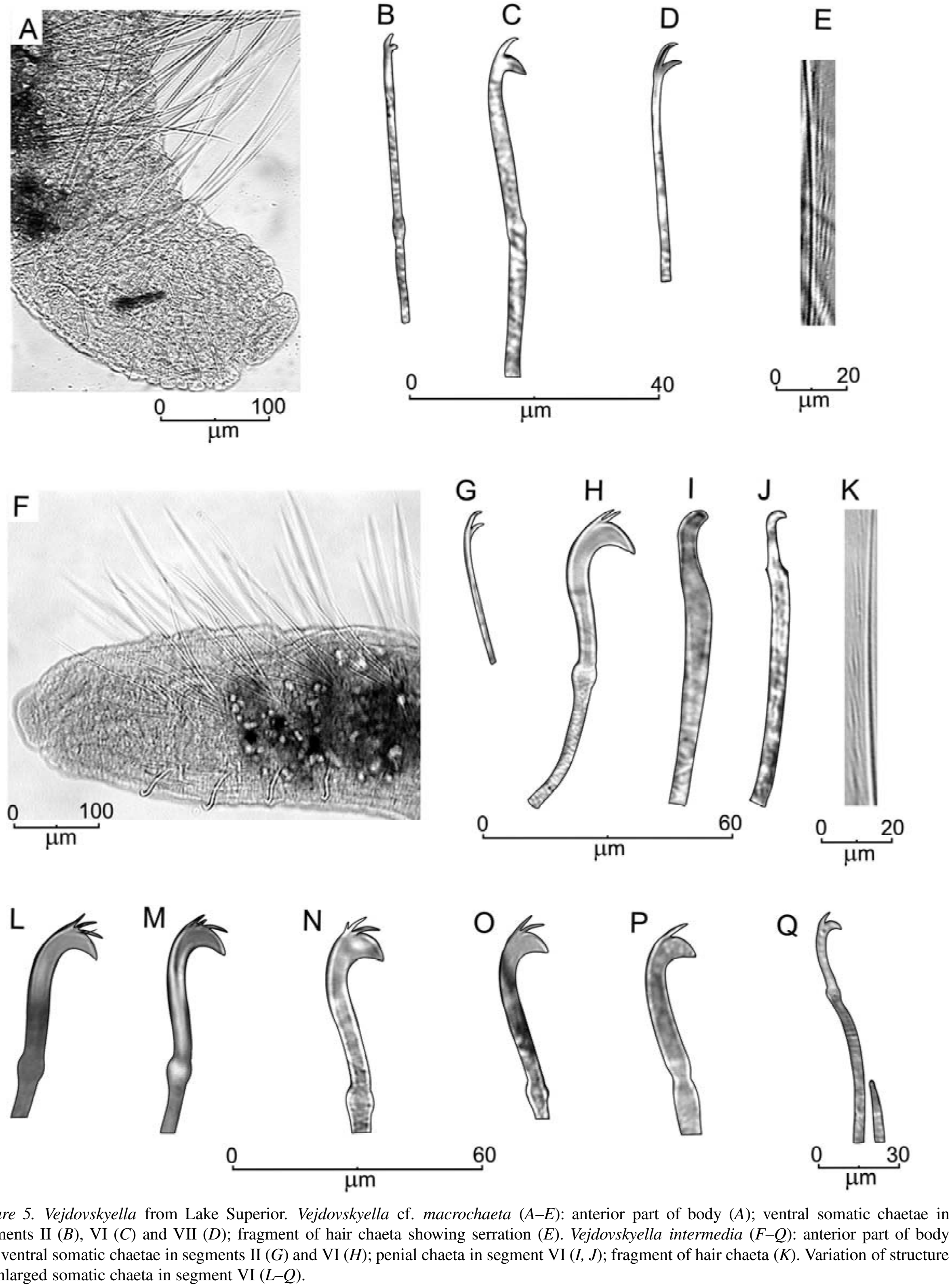

Figure 5. Vejdovskyella from Lake Superior. *Vejdovskyella* cf. *macrochaeta* (*A–E*): anterior part of body (*A*); ventral somatic chaetae in segments II (*B*), VI (*C*) and VII (*D*); fragment of hair chaeta showing serration (*E*). *Vejdovskyella intermedia* (*F–Q*): anterior part of body (*F*); ventral somatic chaetae in segments II (*G*) and VI (*H*); penial chaeta in segment VI (*I, J*); fragment of hair chaeta (*K*). Variation of structure of enlarged somatic chaeta in segment VI (*L–Q*).

Table 1. Occurrence of seven nonindigenous invertebrate species in the Great Lakes as of 2001. Species arranged chronologically by date of first discovery in the Great Lakes. Locations as in Figure 2

Taxonomic group	Species name	Year of discovery in the GL	Known range in the Great Lakes basin	Recent occurrence in Lake Superior
Amphipod	*Gammarus fasciatus*	1874	all GL excluding north-central Lake Superior [1,2]	locations 1-9
Bivalve	*Pisidium moitessierianum*	1895	St. Clair River – Lake Erie drainage [3]	location 5
Bivalve	*Pisidium amnicum*	1899	Lake Huron – St. Lawrence River [4]	location 7
Bivalve	*Sphaerium corneum*	1924	lower GL [4]	location 7
Oligochaete	*Ripistes parasita*	1980	North Channel, Lake Huron [5]; Marquette Co.[6] and Thunder Bay [7], Lake Superior; New York state river drainages [8]	locations 3, 4, 6, 7, 9
Gastropod	*Potamopyrgus antipodarum*	< 1991	Lake Ontario [9]	location 7
Amphipod	*Echinogammarus ischnus*	1994	all GL excluding Lake Superior and north-central Lake Huron [10–12]	location 7

Reference sources: 1. Holsinger, 1976; 2. Mills et al., 1993; 3. Korniushin et al., 2001; 4. Clarke, 1981; 5. Barton & Griffiths, 1984; 6. Hiltunen & Klemm, 1985; 7. Montz, 1988; 8. Simpson & Abele, 1984; 9. Zaranko et al., 1997; 10. Witt et al., 1997; 11. van Overdijk et al., 2003; 12. Vanderploeg et al., 2002.

considered native to this basin. The former species was previously known to occur in this lake, while the latter was recorded throughout the basin except in Lake Superior (Spencer, 1980). We detected populations of *V. intermedia* on sand and silty-sand substrata at depths ranging between 4.5 and 18.7 m (see Table 1). These populations included sexually mature individuals and immature non-budding and budding specimens, indicating that this species is likely established (Fig. 4). Densities ranged between 40 and 700 individuals m^{-2}. We also detected an additional anomalous form of *Vejdovskyella*, which has not been described from North America. This form, possessing morphological features of both *V. intermedia* and Eurasian *V. macrochaeta*, co-occurred with *V. intermedia* on silty sand at 18.7 m depth, offshore from Duluth on 21 August 2001. This form is identifiable as *V. macrochaeta* by its possession of a single upper tooth of enlarged chaetae in segment VI and several subsequent segments (Fig. 5C–D), while those of *V. intermedia* have two to three replicated upper teeth (Hrabě, 1954; Chekanovskaya, 1962; Semernoy & Timm, 1994). Based on the presence of ventral chaetae in segments IV–V and the absence of eyes, it is ascribable to *V. intermedia* (Fig. 5A); however it is distinguished from *V. intermedia* by its possession of bifid enlarged crotchets in segment VI (as above). Some morphological characteristics (e.g., position of the nodules in ventral chaetae VI; length of ventral chaetae II – V) found in the present specimen are also inconsistent with descriptions of *V. comata*, a species lumped with *V. macrochaeta* by North American authorities (Brinkhurst & Kathman, 1983; Kathman & Brinkhurst, 1998). We collected only a single immature individual (0.8 mm long) and were therefore unable to examine its penial chaetae.

We document for the first time the penial chaetae (in segment VI) of mature *V. intermedia*, which are simple-pointed and crescent-shaped, resembling those described for *V. macrochaeta* (Chekanovskaya, 1962). This newly described characteristic of *V. intermedia* supports Hrabě's (1954) contention that *V. intermedia* and *V. macrochaeta* are one species. Moreover, we observed extensive intra-lake variation in somatic chaetae of *V. intermedia* (Fig. 5F–H). One or two replicated upper teeth (of various size and arrangement) were typically present in enlarged ventral crotchets of segment VI, and two upper teeth in enlarged ventral crotchets of the following segment. However, the structure of the distal ends of enlarged ventral crotchets was variable among, and even within, individuals (Fig. 5L–Q).

Arrangement of somatic and genital chaetae in the ventral bundles of *V. intermedia* is documented for the first time here (Fig. 6). Frequency of occurrence of the enlarged somatic chaetae gradually declined from segment VI to IX. One of 55 individuals examined possessed an enlarged bifid crotchet in one ventral bundle of segment X combined with an ordinary somatic chaeta in another bundle.

Using material from this study, Dr R. Hershler (Smithsonian Institution, Washington, D.C., pers. comm.) has identified a mollusc species new for science (Gastropoda: Hydrobiidae). This species was

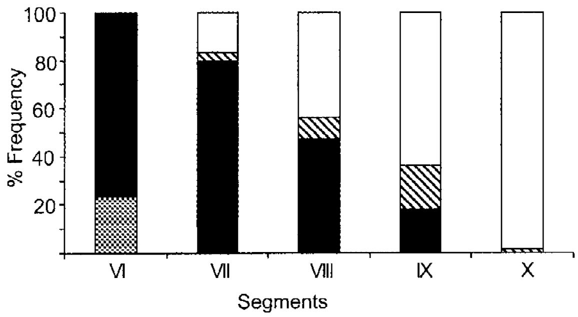

Figure 6. Ventral chaetae of *Vejdovskyella intermedia* from Lake Superior in segments VI–X (55 individuals): penial (▩), enlarged somatic (■), enlarged and ordinary somatic (▧), and ordinary somatic (□).

identified as a member of the genus *Marstonia* based on its shell morphology, structure of the operculum and radula, anatomy of the male verge and DNA sequences (R. Hershler, pers. comm.). The new species was distributed throughout the littoral belt of Lake Superior (Appendix II). It is possible that some previous records of *Marstonia lustrica* (as *M. decepta*; Clarke, 1981) in Lake Superior and the other Great Lakes pertain to its newly identified congener.

Why so few NIS?

Historically, ~10% of the Great Lakes' NIS were initially recorded in Lake Superior (Appendix III). The scarcity of NIS in Lake Superior is paradoxical when compared with the lower Great Lakes, as it receives disproportionately more ballast water discharges than any other of these lakes. Several factors may contribute to this pattern: (*i*) bias in research efforts to survey and identify NIS; (*ii*) lower levels of disturbance to facilitate invasions; (*iii*) lower concentrations of viable propagules supplied by shipping due to a longer voyage duration, or because alternative entry vectors are less significant than in the lower lakes; (*iv*) mismatches of Lake Superior's physicochemical characteristics with physiological tolerances, habitat adaptations and life history strategies of potential NIS; (*v*) food limitation associated with low productivity; (*vi*) biotic resistance of resident species; and (*vii*) lack of facilitation of new NIS by resident species.

Because Lake Superior is zoogeographically less explored than the lower lakes, a research bias could account for its under-representation as a site of initial discovery of Great Lakes' NIS. In particular, the prevalence of cryptic invaders in the lake is likely under-appreciated because few genetic investigations have been conducted in this lake relative to the lower Great Lakes. Historically, joint application of morphological and genetic techniques permitted recognition of several intercontinental introductions to the lower Great Lakes, including the cladocerans *Daphnia galeata* (as *D. galeata galeata*) and *Bosmina maritima* and the mussel *Dreissena bugensis* (May & Marsden, 1992; Taylor & Hebert, 1993; De Melo & Hebert, 1994). All of these introductions likely occurred via ballast water discharge from commercial ships. The Eurasian *D. galeata* has hybridized in the lower Great Lakes with native *D. mendotae* (=*D. galeata mendotae*), generating individuals with low-round helmets (Taylor & Hebert, 1993). We observed a similar round-head phenotype (designated as *D. mendotae*; Appendix I) in the inshore habitats of Lake Superior. Although this may raise the possibility of *D. galeata* introduction to Lake Superior, helmet shape variation could also be due to cyclomorphosis. Only genetic analysis can determine whether the head shape character is genetically-based.

Mapping sites of the first discovery of NIS in the Great Lakes' basin revealed four 'invasion hotspots', featuring >1 NIS per 1000 km^2, one of which is the western end of Lake Superior adjacent to the St. Louis River estuary (Grigorovich et al., 2003). Because of its more pronounced climatic match with NIS sources relative to Lake Superior's habitats, this estuary likely provides more suitable physical-chemical conditions for colonising NIS. During the publication of this paper, several additional NIS (including two new to Lake Superior) have been discovered in the St. Louis River estuary, which may be the source for invaders to Lake Superior (I.A. Grigorovich, unpublished data).

If invasions are facilitated by disturbance (i.e., 'disturbance' hypothesis), Lake Superior is likely to support fewer invaders than the lower Great Lakes because cultural eutrophication and other man-made stresses are not nearly as prevalent as in other lakes (Munawar, 1978). Extensive use of Lake Superior for shipping activities and ballast water discharge by commercial ships is, however, inconsistent with the view that the lake is 'undisturbed'. Ship-borne trade into Lake Superior has established 'invasion corridors', facilitating global transfer of propagules (Ricciardi & MacIsaac, 2000; MacIsaac et al., 2001; Berg et al., 2002).

The 'propagule pressure' hypothesis attributes invasion outcome to propagule supply (MacIsaac et al., 2002; Colautti et al., 2003). While Lake Superior seemingly receives a disproportionately large number of NIS propagules from overseas vessels (Grigorovich et al., 2003), the long transit time required to reach this lake could considerably reduce survivorship of inoculants in ballast tanks as this typically declines exponentially with trip duration (Wonham et al., 2001). Lake Superior therefore may receive fewer live propagules than the lower Great Lakes, despite being the most common destination of discharged ballast water (Colautti et al., 2003). Nevertheless, genetic evidence suggests that zebra mussels may have established in the lake as a result of transoceanic introduction directly from overseas rather than from lower Great Lakes' sources (Stepien et al., 2002). Repeated invasions of Lake Superior by *Bythotrephes* may also have involved direct propagule transferral from overseas sources (Berg et al., 2002). Occurrence of new NIS in the vicinity of international ports on Lake Superior (Thunder Bay, Duluth and Superior) is consistent with the pattern of ballast water discharge from both the transoceanic and 'laker' fleets (Lake Carriers' Association, 1999; Grigorovich et al., 2003).

Alternatively, distributional patterns of some NIS may reflect changes in entry vectors and resultant propagule supply over time. Prior to our study, the nonindigenous sphaeriids *Pisidium moitessierianum*, *P. amnicum* and *Sphaerium corneum*, discovered in the Great Lakes basin between 1895 and 1924, were thought to remain narrowly distributed within the basin of the lower Great Lakes and the St. Lawrence River (e.g., Clarke, 1981). This distributional pattern was attributed to a shift in transport vectors from those associated with solid ballast (used prior to 1900; Mills et al., 1993) to those associated with ballast water (Grigorovich et al., 2000a). Such a shift could decrease or preclude the uptake of sphaeriids by ships. For example, no sphaeriids have been collected in ballast tanks of ballasted or NOBOB vessels (e.g., Aquatic Sciences, 1996; S. Bailey and C. van Overdijk, University of Windsor, Windsor, Ont., unpublished data). Results from our study indicated that these sphaeriids have cryptically invaded Lake Superior, possibly in the early 1900s. Other NIS may have gained entry via alternative entry mechanisms (e.g., hull fouling), which are less significant in Superior than in the lower lakes (Mills et al., 1993). Likewise, discharge of some ballast water prior to entering connecting channels could contribute NIS to the lower Great Lakes even though records of ballast water discharge may indicate a Lake Superior destination.

Physical and chemical aspects of the lake may also retard establishment of NIS. For example, Lake Superior's calcium concentration ($\sim$12 mg l^{-1}) is below the 15 mg l^{-1} threshold necessary for survival of *Dreissena* (reviewed in Vanderploeg et al., 2002). Lake Superior is much colder than many of the global ports that serve as species donors, potentially creating an environmental mismatch between source and destination regions. Lake Superior's open-water temperatures seldom increase above 12 °C. This is below the physiological minimum for gonad growth and reproduction of *Dreissena polymorpha* and some other invaders originating from warm-water habitats (Vanderploeg et al., 2002). Nevertheless, recent records of *D. polymorpha* in the littoral habitats around Lake Superior (U.S. Geological Survey, 2002; this study) suggest that its range is expanding in coastal areas and embayments where its thermal requirements are probably met. Two other 'warm-water' NIS – *Potamopyrgus antipodarum* and *Echinogammarus ischnus* – were found colonizing coastal, shallow-water habitats of Lake Superior that warm extensively during summer months. Their distributions appear to be strongly influenced by lake surface water temperature, which, in turn, is governed by lake morphometry and movement of water masses. It remains to be determined whether these species can persist in Lake Superior given its thermal nature.

Surprisingly, surveys conducted in Lake Superior failed to detect the presence of the quagga mussel *Dreissena bugensis* (U.S. Geological Survey, 2002; this study). This mussel is capable of spawning at 9 °C and is observed to proliferate in the profundal zones of the lower Great Lakes where temperatures are constantly 4–9 °C (Claxton & Mackie, 1998; Vanderploeg et al., 2002). Considering *Dreissena bugensis*' ability to survive under very low food and thermal conditions (Stoeckmann, 2003), its colonization of Lake Superior is anticipated.

NIS capable of cyclic parthenogenesis (e.g., cercopagids) tend to shorten the duration of parthenogenetic reproduction at low temperatures, switching to sexual reproduction with resultant resting egg production (Rivier & Grigorovich, 1999; Grigorovich et al., 2000b). This reproductive strategy may predispose invaders originating from warm-water habitats to a reduced asexual reproductive output in Lake Superior than in the lower lakes, possibly resulting in a lower probability of establishment in this lake. Regardless, the high capacities for asexual reproduction in the two newly recorded NIS in Lake Superior, the gastropod *Potamopyrgus antipodarum* and the oligochaete *Ripistes parasita*, appear to have fostered their colonisation of shallow littoral regions of the lake.

Lake Superior's high ratio of profundal-limnetic to littoral zone may reduce habitat heterogeneity available to NIS relative to the lower lakes (e.g., Munawar, 1978). Many NIS with opportunities to colonize Lake Superior may not meet all of their life history requirements owing to thermal or other conditions in the lake. For example, resistant life stages (e.g., resting eggs) of some species (e.g., *Bythotrephes*) may remain viable in lake sediments for some years, facilitating invasion success (Rivier & Grigorovich, 1999). Nevertheless, under unfavourable environmental conditions (e.g., low temperature, unsuitable substrata) these eggs may not be exposed to appropriate cues required for hatching (Rivier & Grigorovich, 1999). The constant low temperature of Lake Superior's near-bottom waters may reduce or prevent emergence of some 'warm-water' NIS from resting eggs (e.g., *Cercopagis pengoi*, *Daphnia lumholtzi*), thereby lowering the probability of their successful establishment in this lake.

Lake Superior's oligotrophic nutrient state, limited primary productivity and habitat homogeneity relative to the lower lakes may limit the number and types of species capable of surviving in the lake. For example, the lack of required habitats or forage resources in the lake may impede survival and establishment of some NIS, particularly those feeding on phytoplankton, such as the sphaeriid clams, *Pisidium henslowanum* and *P. supinum*. These species exhibit strategies for feeding in shallow-water habitats of rivers and lakes, where food resources are more available than in the deep-water areas (Stadnichenko, 1984; Grigorovich, 1991). These clams probably cannot meet their energy needs by feeding solely on seston available in Lake Superior, in contrast to the native 'profundal' specialists which, in addition to filter feeding, consume organic matter and bacteria from deposited sediments (McMahon & Bogan, 2001).

The 'biotic resistance' hypothesis invokes negative interactions among NIS and resident species in determining invasion outcome (Ricciardi, 2001). Under the lake's environmental conditions, native species may have some competitive advantage over NIS, thereby permitting the native fauna to resist invasion. Yet evidence for such interactions in the Great Lakes, and in Lake Superior in particular, is uncertain (reviewed in Ricciardi, 2001; but Mackie, 1999; van Overdijk et al., 2003).

The 'facilitative interaction' hypothesis proposes that the establishment of 'keystone' NIS may facilitate the introduction of subsequent invaders through mutualistic or commensal interactions (Ricciardi, 2001). It is possible that such relationships among new and already resident NIS are more common or stronger in the lower Great Lakes than in Lake Superior, possibly owing to higher abundances of 'keystone' NIS like *Dreissena* spp. in the lower lakes. Nevertheless, there exist several examples of facilitative interactions among invaders in Lake Superior. For example, exploitative parasite-host relationships promoted the introduction of five parasite species with their coevolved host (i.e., ruffe *Gymnocephalus cernuus*) in Lake Superior (Pronin et al., 1998). In a similar manner, established populations of *D. polymorpha* likely facilitated – via spatial and trophic relationships – the subsequent establishment of the amphipod *Echinogammarus ischnus* (Thunder Bay Harbour), round goby *Neogobius melanostomus* (Duluth and Superior Harbours) and tubenose goby *Proterorhinus marmoratus* (Duluth Harbour) (Vanderploeg et al., 2002; U.S. Geological Survey, 2002; this study).

Need for genetic reappraisal

Faunal surveys performed in Lake Superior since the early 1800s have identified nine NIS before they were recorded elsewhere in the Great Lakes (Appendix III). These records, based on morphological analyses, provide a historical context for introduction of NIS into this lake. Most cases involved species that are distinct in morphology from resident taxa (see Grigorovich et al., 2003 for detail). Discerning nonindigenous and native taxa on morphological grounds alone may be difficult, particularly for poorly studied or 'cryptic' (i.e., those with limited morphological differentiation) taxa (e.g., oligochaetes; Spencer, 1980). Yet some representatives of the Great Lakes' fauna are deemed cosmopolitan based on morphological grounds (e.g., oligochaetes; Spencer & Hudson, 2003). As a consequence, the extent of their introductions is likely underestimated. Results from our study indicated that several NIS with prior invasion history in the lower Great Lakes have cryptically invaded Lake Superior, but remained undetected until now. Application of genetic techniques may further expand the number of recognized NIS in Lake Superior.

Two species with lake-wide distributions (e.g., *Vejdovskyella intermedia*, *Marstonia* sp. n.) were first discovered in this study, indicating that Lake Superior's native fauna is still inadequately studied. Thus, Lake Superior's faunal diversity must be further explored in order to comprehend the full extent of anthropogenic impacts on the lake ecosystem.

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Appendix 1. Zooplankton taxa collected from Lake Superior during June and August 2001, arranged phylogenetically

Taxon	Sault Ste. Marie	Munising	Marquette	Copper Harbor	Superior	Duluth	Thunder Bay	Marathon	Wawa
ROTIFERA									
Monogononta									
Ascomorpha ecaudis	-	-	-	-	-	+	-	-	-
Ascomorpha ovalis	+	-	+	+	-	-	-	-	-
Ascomorpha saltans	-	-	-	-	-	-	+	+	-
Asplanchna priodonta	+	+	+	+	+	+	+	+	+
Brachionus angularis	-	-	-	-	+	-	-	-	-
Brachionus calyciflorus	-	-	-	+	-	-	-	-	-
Cephalodella gibba	+	-	-	-	-	-	-	-	-
Collotheca ?pelagica	+	+	+	+	+	+	+	+	+
Conochilus hippocrepis	-	+	+	+	+	-	+	-	-
Conochilus unicornis	+	+	+	+	+	+	+	+	+
Dicranophorus cf. *forcipatus*	-	-	-	-	-	-	+	-	-
Encentrum ?saundersiae	-	-	-	-	+	-	+	-	-
Euchlanis meneta	-	+	-	-	+	-	-	-	-
Gastropus hyptopus	-	-	-	+	-	-	+	+	-
Gastropus stylifer	+	+	-	+	-	-	-	-	+
Kellicottia longispina	+	+	+	+	+	+	+	+	+
Keratella cochlearis	+	+	+	+	+	+	+	+	+
Keratella crassa	+	+	+	+	+	+	+	+	+
Keratella earlinae	-	+	+	+	+	+	+	+	+
Keratella hiemalis	-	-	-	-	+	-	-	-	-
Keratella quadrata	-	-	-	+	-	+	+	-	-
Lecane bulla	-	-	-	-	+	-	-	-	-
Lecane cf. *copeis*	-	-	-	-	-	-	+	-	-
Lecane cf. *depressa*	-	-	-	+	-	-	-	-	-
Lecane lunaris	-	-	-	-	-	-	-	-	+
Notholca foliacea	-	+	+	-	+	+	+	+	-
Notholca laurentiae	-	-	+	+	-	-	+	+	-
Notholca squamula	-	+	+	+	+	+	+	+	+
Notommata copeus	-	-	-	-	-	+	-	-	-
Platyias quadricornis	-	-	-	-	-	-	+	-	-
Ploesoma hudsoni	-	+	-	-	+	+	+	+	+
Ploesoma truncatum	+	+	+	-	+	+	+	+	+
Polyarthra dolichoptera				+					
Polyarthra major	+	+	+	+	+	+	+	+	+
Proales ?sordida	+	-	-	-	-	-	-	-	-
Stephanoceros ?fimbriatus	+	-	-	-	-	-	-	-	-
Synchaeta asymmetrica	-	+	+	-	+	+	+	+	+
Synchaeta grandis	-	+	+	-	-	-	+	-	-
Synchaeta lackowitziana	+	+	+	+	+	+	+	+	+
Synchaeta stylata	+	+	+	+	+	+	+	+	+
Trichocerca cf. *cylindrica*	-	-	-	+	-	-	-	-	-
Trichocerca cf. *mucosa*	-	-	-	-	-	+	+	-	-
Trichocerca multicrinis	-	-	-	-	+	+	-	-	-
Trichocerca porcellus	+	-	-	-	-	+	+	-	-
Trichocerca pusilla	-	-	-	+	+	+	-	-	-
Trichocerca sp.	-	-	-	-	+	-	-	-	+
Trichotria pocillum	-	-	-	-	+	-	-	-	-
Trichotria tetractis	+	-	-	-	-	-	-	-	-
Bdelloidea, unidentified	-	+	-	-	-	+	+	+	+

Appendix 1. contd.

ARTHROPODA									
Branchiopoda									
Alona (*Biapertura*) *affinis*	-	-	-	-	-	+	-	-	-
Alona ?*costata*	-	-	+	-	-	-	-	-	-
Alona guttata	-	-	-	-	-	-	-	+	-
Alona ?*rectangula*	-	-	-	-	+	-	-	-	-
Alona sp.	+	+	-	+	-	-	-	+	-
Alona (*Biapertura*) sp.	-	-	+	-	-	-	-	+	-
Anchistropus emaginatus	-	-	-	-	+	-	-	-	-
Bosmina coregoni §	-	-	-	-	+	+	-	-	-
Bosmina liederi	+	+	+	+	+	+	+	+	+
Bythotrephes longimanus §	+	+	+	+	+	+	+	+	+
Camptocercus rectirostris	-	-	-	-	-	-	-	+	-
Ceriodaphnia lacustris	-	-	-	-	+	-	-	-	+
Ceriodaphnia pulchella	-	-	-	-	+	+	-	-	-
Chydorus gibbus	-	+	+	-	+	+	+	+	+
Chydorus ?*sphaericus*	+	+	-	+	-	+	-	-	+
Chydorus sp.	-	+	+	-	+	+	+	-	
Daphnia mendotae	+	+	-	+	+	+	+	+	+
Daphnia retrocurva	-	+	-	+	+	+	+	+	+
Diaphanosoma birgei	-	+	-	-	+	+	-	-	-
Eurycercus lamellatus	-	-	+	-	-	+	-	-	-
Holopedilum gibberum	+	+	+	+	+	+	+	+	+
Ilyocryptus sordidus	-	-	+	-	+	-	-	-	-
Leptodora kindti	-	+	-	-	+	+	+	-	-
Leydigia quadrangularis	-	-	-	-	+	-	-	-	-
Monospilus dispar	-	-	-	-	+	+	+	-	-
Polyphemus pediculus	+	-	-	-	-	-	-	-	-
Rhynchotalona falcata	-	-	+	-	-	-	-	-	-
Scapholeberis kingi	-	+	-	-	-	-	-	-	-
Maxillopoda									
Acanthocyclops brevispinosus	-	-	-	-	+	+	-	-	-
Acanthocyclops robustus	-	-	-	-	+	+	+	-	-
Attheyella nordenskioldi	-	-	-	-	-	-	+	-	-
Canthocamptus robertcokeri	-	-	-	-	-	+	-	-	-
Canthocamptus staphylinoides	-	-	+	-	-	-	-	-	-
Diacyclops thomasi	+	+	+	+	+	+	+	+	+
Epischura lacustris	+	+	+	+	+	+	+	+	+
Ergasilus sp.	-	-	-	-	+	-	-	-	-
Eucyclops elegans	-	-	-	-	-	+	-	-	-
Harpacticoida, unidentified	-	-	-	-	+	+	-	-	-
Leptodiaptomus sicilis	+	+	+	+	+	+	+	+	+
Limnocalanus macrurus	+	+	+	+	+	+	+	+	+
Mesocyclops edax	-	-	-	+	+	+	+	+	-
Microcyclops rubellus	-	-	-	-	+	-	-	-	-
MOLLUSCA									
Bivalvia									
Dreissena veligers §	-	-	-	-	+	+	-	-	-
Total	28	36	33	33	54	49	44	34	30

Note: Nonindigenous species are marked with §. Presence of species is indicated by +.

Appendix 2. Benthic and near-bottom taxa collected from Lake Superior during June and August 2001, arranged phylogenetically

Taxon	Sault Ste. Marie	Munising	Marquette	Copper Harbor	Superior	Duluth	Thunder Bay	Marathon	Wawa
PORIFERA									
Demospongiae, unidentified	-	-	-	-	-	+	-	-	-
CNIDARIA									
Hydrozoa									
Cordylophora caspia §	-	-	-	-	-	+	-	-	-
Hydra sp.	-	-	-	-	-	+	-	-	-
PLATYHELMINTHES									
Turbellaria, unidentified	-	-	+	-	+	-	-	+	-
Mesostoma sp.	-	-	-	+	-	-	-	-	-
NEMATODA									
Unidentified	+	+	+	+	+	+	+	+	-
BRYOZOA									
Phylactolaemata									
Cristatella mucedo	-	+	-	-	-	-	-	-	+
Lophopodella carteri §	+	-	-	-	-	-	-	-	-
Paludicella articulata	+	-	-	-	-	+	+	-	-
Pectinatella magnifica	-	-	-	-	+	-	-	-	-
Plumatella emarginata	-	-	-	-	+	+	-	-	-
Plumatella sp.	+	+	+	-	+	+	+	-	-
?Pottsiella erecta	+	-	-	-	-	-	-	-	-
ANNELIDA									
Polychaeta									
Manayunkia speciosa	-	-	-	-	-	-	+	-	-
Serpulidae, unidentified	-	-	-	-	-	-	+	-	-
Aphanoneura									
Aeolosoma sp.	+	-	-	-	-	-	-	-	-
Oligochaeta									
Arcteonais lomondi, CMN	+	+	+	+	-	-	+	-	-
Aulodrilus limnobius, CMN	-	-	-	+	-	+	-	-	-
Aulodrilus pigueti, CMN	-	-	-	-	+	-	-	-	-
Aulodrilus pluriseta, CMN	-	-	-	-	+	+	-	-	-
Chaetogaster diaphanus	-	-	-	-	-	+	-	-	-
Chaetogaster sp.	-	-	-	-	-	+	-	-	-
Dero digitata	-	-	-	-	-	+	-	-	-
Eiseniella tetraedra	-	-	-	+	-	-	-	+	-
Enchytraeidae, unidentified	-	-	-	-	-	-	+	-	-
Limnodrilus hoffmeisteri, CMN	+	-	-	-	+	-	+	-	-
Limnodrilus maumeensis, CMN	-	+	-	-	+	-	-	-	-
Limnodrilus profundicola	-	-	-	-	-	+	-	-	-
Limnodrilus udekemianus, CMN	-	-	-	-	-	+	+	-	-
Lumbriculus variegatus, CMN	-	-	-	-	-	-	+	-	-
Mesenchytraeus sp.	-	-	-	-	-	-	+	-	-
Naididae, unidentified	-	-	-	+	-	+	-	+	-
Nais elinguis	-	-	-	+	-	-	-	-	-
Nais pardalis	-	-	-	+	-	-	-	-	-
Nais pseudobtusa	-	-	-	+	-	-	-	-	-
Nais variabilis	-	-	-	+	-	+	-	-	-
Ophidonais serpentina	-	-	-	-	-	-	+	-	-
Piguetiella michiganensis	-	-	-	-	-	+	-	-	-

Appendix 2. contd.

Potamothrix moldaviensis §	-	+	+	-	+	+	+	-	-
Potamothrix vejdovskyi §	-	-	-	-	-	-	+	-	-
Pristina breviseta	-	-	-	-	-	-	+	-	-
Pristina sp.	-	-	-	-	-	-	+	-	-
Ripistes parasita §, CMN	-	-	+	+	-	+	+	-	+
Slavina appendiculata, CMN	-	-	-	-	-	+	+	-	-
Spirosperma ferox §, CMN	+	+	+	+	+	+	+	+	-
Spirosperma nikolskyi	-	-	-	+	-	-	-	-	-
Stylaria lacustris	-	-	-	+	-	-	+	-	-
Stylodrilus heringianus §	+	+	+	+	+	+	+	+	+
Tasserkidrilus kessleri, CMN	+	+	-	-	-	+	+	+	-
Tubifex ignotus, CMN	-	-	-	-	+	-	+	+	-
Tubifex tubifex	-	+	-	-	+	+	+	-	-
Tubifex sp.	-	+	-	-	+	-	+	-	-
Tubificidae with hair chaetae, unidentified	+	-	-	+	+	+	+	+	-
Tubificidae without hair chaetae, unidentified	+	+	-	-	+	+	+	-	-
Quistadrilus multisetosus	-	-	-	-	-	-	+	-	-
Uncinais uncinata, CMN	-	-	+	-	-	-	+	+	-
Varichaetadrilus angustipenis	-	-	-	-	-	-	+	-	-
Vejdovskyella comata	-	-	-	-	-	+	-	-	-
Vejdovskyella intermedia, CMN	+	-	-	+	+	+	+	-	-
Vejdovskyella cf. *macrochaeta*, CMN	-	-	-	-	-	+	-	-	-
Hirudinea									
Dina dubia	-	+	-	-	-	-	-	-	-
Glossiphonia complanata	-	+	-	-	-	-	-	-	-
Helobdella stagnalis	-	+	+	+	+	-	+	-	-
ARTHROPODA									
Arachnida									
Aranei, unidentified	-	-	-	+	-	-	-	-	-
Hydrachnida, unidentified	-	+	+	+	+	+	+	+	-
Branchiopoda									
Daphnia ephippia	-	+	+	-	+	+	-	+	-
Latona setifera	-	-	-	-	-	+	+	-	-
Maxillopoda									
Calanoida, unidentified	+	+	-	-	+	+	+	+	+
Cyclopoida, unidentified	-	+	-	+	+	+	+	+	-
Harpacticoida, unidentified	-	-	+	+	-	+	+	+	-
Ostracoda, unidentified	+	+	+	+	+	+	+	+	-
Malacostraca									
Asellus communis	-	+	+	+	-	-	+	+	-
Asellus sp.	-	+	-	+	-	-	+	-	-
Diporeia gr. *brevicornis*	-	-	-	+	-	-	-	-	-
Diporeia gr. *filicornis*	+	+	+	+	-	+	+	+	+
Echinogammarus ischnus§	-	-	-	-	-	-	+	-	-
Gammarus fasciatus §, CMN	+	+	+	+	+	+	+	+	+
Gammarus pseudolimnaeus	-	-	-	+	-	-	+	-	-
Gammarus sp.	-	-	+	+	-	-	-	-	-
Hyalella azteca	-	+	-	+	-	-	-	+	-
Lirceus lineatus	-	-	+	+	-	-	-	-	-
Mysis relicta	-	-	-	+	-	-	+	+	-

Appendix 2. contd.

Insecta									
Chironomidae, unidentified	+	+	+	+	+	+	+	+	+
Coleoptera, unidentified	-	-	-	-	-	-	+	-	-
Empididae, unidentified	-	-	-	-	+	-	-	+	+
Ephemeroptera, unidentified	+	+	-	-	-	-	-	-	-
Heleidae, unidentified	-	+	-	+	+	-	-	-	+
Heteroptera, unidentified	-	-	-	-	-	+	-	-	-
Hexagenia sp.	-	+	-	-	-	-	-	-	-
Odonata, unidentified	-	-	-	-	+	-	-	-	-
Podura sp.	-	-	-	-	-	+	-	-	-
Sisyra sp.	-	-	-	+	-	-	-	-	-
Trichoptera, unidentified	-	-	+	+	+	-	+	+	+
TARDIGRADA									
Unidentified	-	-	-	-	-	-	+	-	-
MOLLUSCA									
Gastropoda									
Amnicolinae, unidentified, NMNH	-	+	-	-	+	-	+	+	-
Fossaria decampi	-	-	-	+	-	-	-	-	-
Fossaria modicella	-	+	-	+	-	-	-	-	-
Fossaria parva	-	-	-	+	-	-	-	-	-
Fossaria sp.	-	-	-	+	+	-	-	-	-
Gyraulus circumstriatus	-	-	+	+	+	-	+	-	-
Gyraulus deflectus	-	-	+	+	-	-	+	-	-
Gyraulus parvus	-	-	-	+	+	-	+	-	-
Helisoma anceps	-	-	+	+	-	-	-	+	-
Helisoma sp.	-	-	-	+	-	-	-	-	-
Lymnaea sp.	-	-	-	-	-	-	+	-	-
Marstonia lustrica, NMNH	-	-	-	+	-	-	-	-	-
Marstonia sp. n., NMNH	-	-	+	+	+	-	+	+	
Physella sp.	-	-	-	-	-	-	+	-	-
Pseudosuccinea columella	-	-	-	+	-	-	+	-	-
Potamopyrgus antipodarum §, CMN	-	-	-	-	-	-	+	-	-
Valvata sincera	-	+	+	+	+	-	+	+	-
Valvata tricarinata	-	+	+	+	+	-	+	+	-
Bivalvia									
Dreissena polymorpha §	-	-	-	-	+	-	+	-	-
Musculium lacustre	-	-	-	-	-	-	+	-	-
Musculium ?partumeium	-	-	-	-	-	-	+	-	-
Musculium sp.	-	-	-	-	-	-	+	-	-
Pisidium adamsi, AVKC	-	-	-	-	-	-	+	-	-
Pisidium amnicum§AVKC	-	-	-	-	-	-	+	-	-
Pisidium cf. *casertanum*, AVKC	-	+	-	+	-	+	+	-	-
Pisidium compressum, AVKC	-	-	+	-	+	+	+	-	-
Pisidium conventus, AVKC	+	+	+	+	+	+	+	+	+
Pisidium ferrugineum, AVKC	-	-	+	+	+	-	+	-	-
Pisidium idahoense, AVKC	-	-	-	+	-	-	+	+	-
Pisidium insigne, AVKC	-	-	-	+	-	-	-	-	-
Pisidium lilljeborgi, AVKC	+	+	+	+	-	+	+	+	-
Pisidium milium, AVKC	-	-	-	+	-	-	-	-	-
Pisidium moitessierianum§AVKC	-	-	-	-	+	-	-	-	-
Pisidium nitidum, AVKC	-	+	-	+	-	-	+	+	-
Pisidium simplex, AVKC	-	+	-	-	+	-	-	-	-

Appendix 2. contd.

Pisidium subtruncatum, AVKC	-	-	-	+	+	-	-	-	-
Pisidium ventricosum, AVKC	-	-	-	+	-	-	-	-	-
Pisidium walkeri, AVKC	-	-	-	+	-	-	+	-	-
Pisidium sp.	+	-	+	+	+	+	+	+	+
Sphaerium corneum§, AVKC	-	-	-	-	-	-	+	-	-
Sphaerium nitidum, AVKC	-	-	-	+	-	-	+	+	-
Sphaerium striatinum, AVKC	-	-	-	+	-	-	-	-	-
Sphaerium sp., AVKC	-	-	-	-	-	-	+	+	-
Total	23	37	31	68	44	46	79	35	13

Note: Nonindigenous species are marked with §. Presence of species is indicated by +. Collections, where representative specimens were deposited: CMN, Canadian Museum of Nature, Ottawa, Ontario; AVKC, Alexei V. Korniushin personal collection, Institute of Zoology, National Academy of Sciences, Kiev, Ukraine; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Appendix 3. Nonindigenous and cryptogenic metazoans and protists established in the Laurentian Great Lakes basin since 1800s, arranged chronologically

No.	Taxonomic group	Species name	Year of discovery	Location
1	Pisces	*Carassius auratus*	1700s	pond (LO)
2	Pisces	***Petromyzon marinus***	1830s	Lake Ontario
3	Mollusca	*Elimia virginica*	1850s	Erie Canal (LO)
4	Mollusca	*Bithynia tentaculata*	1871	Lake Michigan
5	Pisces	***Alosa pseudoharengus***	1873	Lake Ontario
6	Pisces	***Oncorhynchus tshawytscha***	1873	all the Great Lakes but LS
7	Crustacea	***Gammarus fasciatus***	1874	Grand Rapids (LM)
8	Pisces	***Oncorhynchus mykiss***	1876	Lake Huron
9	Pisces	***Cyprinus carpio***	1879	pond (LO)
10	Pisces	***Salmo trutta***	1883	Lake Ontario
11	Mollusca	***Pisidium moitessierianum*** (as *P. punctatum*)	1895	Portage County (LE)
12	Mollusca	***Pisidium amnicum***	1899	Lake Ontario
13	Mollusca	*Radix auricularia*	1901	Lake Michigan
14	Mollusca	*Viviparus georginanus*	1906	river (LM)
15	Pisces	***Osmerus mordax***	1912	Crystal Lake (LM)
16	Mollusca	*Valvata piscinalis*	1913	Lake Ontario
17	Mollusca	*Pisidium henslowanum*	1916	Lake Ontario
18	Mollusca	*Gillia altilis*	1918	Oneida Lake (LO)
19	Annelida	*Potamothrix bavaricus*	1918	Cayuga Lake (LO)
20	Pisces	*Gambusia affinis* (with *G. holbrooki* ?)	1923	Cook County (LM)
21	Mollusca	***Sphaerium corneum***	1924	Lake Ontario
22	Pisces	*Lepomis microlophus*	1928	Indiana lakes (LM)
23	Pisces	*Noturus insignis*	1928	Oswego River (LO)
24	Pisces	*Lepomis humilis*	1929	Lake St. Mary's (LE)
25	Mollusca	*Cipangopaludina chinensis malleata*	1931	Niagara River
26	Cnidaria	*Craspedacusta sowerbyi*	1933	Lake Erie
27	Pisces	***Oncorhynchus kisutch***	1933	Lake Erie
28	Bryozoa	***Lophopodella carteri***	1934	Lake Erie
29	Pisces	*Misgurnus anguillicaudatus*	1939	Shiawassee River (LH)

Appendix 3. contd.

30	Mollusca	*Cipangopaludina japonica*	1940s	Lake Erie
31	Insecta	***Tanysphyrus lemnae***	1943	Unknown
32	Insecta	*Acentropus niveus*	1950	Lake Ontario
33	Pisces	***Morone americana***	1950	Cross Lake (LO)
34	Pisces	*Oncorhynchus nerka*	1950	Lake Ontario
35	Pisces	*Phenacobius mirabilis*	1950	Ohio drainage (LE)
36	Pisces	*Scardinius erythrophthalmus*	1950	drainage (LO)
37	Annelida	*Branchiura sowerbyi*	1951	Kalamazoo River (LM)
38	Annelida	***Potamothrix moldaviensis***	1952	outlet of Lake Ontario
39	Cnidaria	***Cordylophora caspia***	1956	Lake Erie
40	Pisces	***Oncorhynchus gorbuscha***	1956	Current River (LS)
41	Pisces	*Cyprinella lutrensis*	1958	drainage (LM)
42	Mollusca	*Lasmigona subviridis*	1959	Erie Canal (LO)
43	Mollusca	*Pisidium supinum*	1959	Lake Ontario
44	Protista	*Glugea hertwigi* *	1960	Lake Erie
45	Annelida	***Stylodrilus heringianus***	1960	St. Marys River
46	Annelida	***Spirosperma ferox***	1962	Lake Ontario, Cataraqui Bay
47	Annelida	***Potamothrix vejdovskyi***	1965	Lake Erie
48	Crustacea	***Eurytemora affinis***	1961	Lake Erie
49	Pisces	*Lepisosteus platostomus*	1962	Lake Winnebago (LM)
50	Crustacea	***Bosmina coregoni***	1966	Lake Michigan
51	Crustacea	*Skistodiaptomus pallidus*	1967	Lake Ontario
52	Platyhelmithes	*Dugesia polychroa*	1968	Lake Ontario
53	Protista	*Myxosoma cerebralis*	§1968	Ohio drainage (LE)
54	Pisces	*Enneacanthus gloriosus*	1971	Jamesville Reservoir (LO)
55	Crustacea	***Cyclops strenuus***	1972	St. Marys River
56	Crustacea	*Nitocra hibernica*	1973	Lake Ontario
57	Annelida	*Potamothrix hammoniensis*	1976	Lake Michigan, Green Bay
59	Annelida	*Pristina acuminata*	1977	Lake Erie
60	Pisces	*Notropis buchanani*	1979	Thames River (LStC)
61	Annelida	*Daphnia galeata*	1980s	Lake Erie
62	Annelida	***Chaetogaster setosus***	1980	St. Marys River
63	Mollusca	*Corbicula fluminea*	1980	Lake Erie
64	Annelida	***Ripistes parasita***	1980	Lake Huron, North Channel
65	Pisces	*Alosa aestivalis*	1981	Oneida Lake (LO)
66	Crustacea	***Bythotrephes longimanus***	1982	Lake Ontario
67	Annelida	*Gianius aquaedulcis*	1983	Niagara River
68	Crustacea	***Salmincola lotae***x	1985	Lake Superior
69	Pisces	***Apeltes quadracus***	1986	Lake Superior
70	Pisces	***Gymnocephalus cernuus***	1986	Lake Superior
71	Crustacea	*Bosmina maritima*	1988	Lake Michigan
72	Crustacea	*Argulus japonicus* †	1988	Lake Michigan
73	Mollusca	***Dreissena polymorpha***	1988	Lake St. Clair
74	Mollusca	*Dreissena bugensis*	1989	Port Colborne (LE)
75	Pisces	*Alosa chrysochloris*	1989	Lake Michigan, Green Bay
76	Pisces	***Neogobius melanostomus***	1990	St. Clair River
77	Pisces	***Proterorhinus marmoratus***	1990	St. Clair River
78	Mollusca	***Potamopyrgus antipodarum***	1991	Lake Ontario
79	Platyhelminthes	***Dactylogyrus amphibothrium*** ‡	1992	Lake Superior
80	Platyhelminthes	***Dactylogyrus hemiaphibothrium*** ‡	1992	Lake Superior
81	Platyhelminthes	***Neascus brevicaudatus*** ‡	1992	Lake Superior

Appendix 3. contd.

82	Platyhelminthes	***Ichthyocotylurus pileatus*** ‡ ∫	1992	Lake Superior
83	Protista	***Trypanosoma acerinae*** ‡	1992	Lake Superior
84	Crustacea	*Onychocamptus mohammed*	1992	Lake Ontario
85	Crustacea	*Echinogammarus ischnus*	1994	Lake Erie
86	Crustacea	*Neoergasilus japonicus* ff	1994	Lake Huron
87	Protista	*Sphaeromyxa sevastopoli* ¶	1994	St. Clair River
88	Platyhelminthes	*Scolex pleuronectis* ∫	1994	St. Clair River
89	Crustacea	*Heteropsyllus* cf. *nunni*	1996	Lake Michigan
90	Protista	*Acineta nitocrae*+	1997	Lake Erie
91	Crustacea	*Cercopagis pengoi*	1998	Lake Ontario
92	Crustacea	*Schizopera borutzkyi*	1998	Lake Michigan
93	Crustacea	*Nitocra incerta*	1999	Detroit River
94	Crustacea	*Daphnia lumholtzi*	1999	Lake Erie
95	Annelida	*Barbidrilus paucisetus*	2001	Lake Erie
96	Annelida	*Pristina longisoma*	2001	Lake Erie
97	Annelida	*Pristina sima*	2001	Lake Michigan
98	Annelida	*Psammoryctides barbatus*	2001	Lake Erie
99	Annelida	**Stephensoniana trivandrana**	2001	St. Marys River

Note: This compilation of nonindigenous and cryptogenic animals and protists in the Great Lakes updates Mills et al. (1993) report entitled "Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions". Summarized from Cook & Johnson, 1974; Clarke, 1981; Hiltunen & Klemm, 1985; Mills et al., 1993; Kathman & Brinkhurst, 1998; Pronin et al., 1998; Mackie, 1999; Grigorovich et al., 2000; Spencer & Hudson, 2003; van Overdijk et al., 2003 (see Mills et al., 1993; Ricciardi, 2001; Spencer & Hudson, 2003; and Grigorovich et al., 2003 for additional references). Species recorded in Lake Superior and St. Marys River are bold-faced. Species sites in the surrounding drainage basins are ascribed to immediate downstream open-water locations. Keys to locations: LO, Lake Ontario; LE, Lake Erie; LStC, Lake St. Clair; LH, Lake Huron; LM, Lake Michigan; LS, Lake Superior. Parasite and epibiont hosts: * - *Osmerus mordax*; §- *Tubifex tubifex* and salmonids; × - *Lota lota*; † - *Carassius auratus*; ‡ - *Gymnocephalus cernuus*; ∫ - *Neogobius melanostomus*; ff - cyprinids, percids and centrarchids; ¶ - *Proterorhinus marmoratus*; + - *Nitocra* spp.