DISCUSSION / DISCUSSION

Comment on "Rate of species introductions in the Great Lakes via ships' ballast water and sediments"[1]

Janet W. Reid and Patrick L. Hudson

Abstract: The four species of freshwater copepod crustaceans found in ballast water or sediments in ships and characterized as "nonindigenous" to the Laurentian Great Lakes region by Drake and Lodge (Can. J. Fish. Aquat. Sci. **64**: 530–538 (2007)) are all widespread, North American natives. Drake and Lodge's use of these native species to estimate the size of the "source pool" of the richness of potential invasive species resulted in an overestimation of its size. We list the fresh- and brackish-water species of copepods found in or on ships in the Great Lakes and discuss taxonomic and other questions pertaining to some of them. We suggest that *Skistodiaptomus pallidus*, *Cyclops strenuus*, *Salmincola lotae*, *Nitokra incerta*, and *Onychocamptus mohammed* be removed from the current list of nonindigenous copepod and branchiuran species established in the Great Lakes system, leaving seven species: *Eurytemora affinis*, *Megacyclops viridis*, *Neoergasilus japonicus*, *Heteropsyllus nunni*, *Nitokra hibernica*, *Schizopera borutzkyi*, and *Argulus japonicus*.

Résumé : Les quatre espèces de crustacés copépodes d'eau douce trouvées dans les eaux de ballastage ou les sédiments dans les navires et caractérisées de « non indigènes » à la région des Grands Lacs laurentiens par Drake et Lodge (J. Can. Sci. Halieut. Aquat. **64**: 530–538 (2007)) sont toutes des espèces natives de l'Amérique du Nord à large répartition géographique. L'utilisation de ces espèces indigènes par Drake et Lodge dans leur estimation de la taille du « bassin d'origine » de la richesse des espèces envahissantes potentielles mène à une surestimation. Nous dressons une liste des espèces de copépodes d'eaux douce et saumâtre trouvées dans ou sur les navires dans les Grands Lacs et nous discutons de questions taxonomiques ou autres qui concernent certaines d'entre elles. Nous suggérons de retirer *Skistodiaptomus pallidus*, *Cyclops strenuus*, *Salmincola lotae*, *Nitokra incerta* et *Onychocamptus mohammed* de la liste actuelle de copépodes et de branchioures non indigènes établis dans le système des Grands Lacs, ce qui laisse sept espèces, soit *Eurytemora affinis*, *Megacyclops viridis*, *Neoergasilus japonicus*, *Heteropsyllus nunni*, *Nitokra hibernica*, *Schizopera borutzkyi* et *Argulus japonicus*.

[Traduit par la Rédaction]

Drake and Lodge (2007*a*) presented a list of 17 species of small invertebrates found in ballast water in ships entering the Laurentian Great Lakes and characterized all of the species as "nonindigenous" to the Great Lakes. They then used these data to estimate the size of the "source pool" of the richness of potential invasive species. The seven freshwater species that the authors characterized as nonindigenous include one rotifer, one mysid, one ostracode, and four copepods: *Microcyclops rubellus*, *Microcyclops varicans*, *Paracyclops chiltoni*, and *Maraenobiotus insignipes*.

We question the criteria for terming these copepods nonindigenous. The first three occur widely in North America, including the Great Lakes (Hudson and Lesko 2003). *Maraenobiotus insignipes*, although not reported from the Great Lakes proper, is widespread in northern North America (Wilson and Yeatman 1959); a juvenile *Maraenobiotus* sp. was collected in the early 1970s in Lake St. Clair (Hudson and Lesko 2003). Members of this genus are usually found in streams, seeps, and damp moss, so would be unlikely to establish in the Great Lakes proper.

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Table 1. Nonindigenous species of copepod and branchiuran crustaceans established in the Laurentian Great Lakes system.

Species	Native distribution	Year discovered	Lake(s) recorded from	Recent references
Eurytemora affinis	North America, Europe (estuaries); brackish to freshwater	1958	All	Hudson and Lesko 2003; Great Lakes Environmental Research Laboratory (GLERL) 2006
Megacyclops viridis	Europe; freshwater	1989	Superior	Hudson and Lesko 2003; Great Lakes Environmental Research Laboratory (GLERL) 2006
Neoergasilus japonicus	East Asia; introduced into Cuba and Europe; ectoparasite of freshwater fishes	1994	Huron	Grigorovich et al. 2003; Great Lakes Environmental Research Laboratory (GLERL) 2006
Heteropsyllus nunni	East coast of North America (estuaries); brackish to freshwater	1996 2000	Michigan St. Clair	Grigorovich et al. 2003; Hudson and Lesko 2003; Holeck et al. 2004; Great Lakes Environmental Research Laboratory (GLERL) 2006
Nitokra hibernica	Eurasia; brackish to freshwater	1973	Huron, Michigan, Erie, Ontario	Grigorovich et al. 2003; Hudson and Lesko 2003; Holeck et al. 2004; Great Lakes Environmental Research Laboratory (GLERL) 2006
Schizopera borutzkyi	Ponto-Caspian; brackish to freshwater	1998 2003	Michigan Erie	Grigorovich et al. 2003; Hudson and Lesko 2003; Holeck et al. 2004; Great Lakes Environmental Research Laboratory (GLERL) 2006
Argulus japonicus	Asia; now found on most continents; ectoparasite of freshwater fishes	1989	Huron, Michigan, Erie	Mills et al. 1993; Grigorovich et al. 2003; Hudson and Lesko 2003; Great Lakes Environmental Research Laboratory (GLERL) 2006

The analysis of these collection data to estimate the rate of species introduction into the Great Lakes appears to us to suffer from mischaracterization of a high proportion of the freshwater species as nonindigenous. The result is a serious overestimation of the pool of potential invaders. We encourage Drake and Lodge to recalculate their estimates after consulting with taxonomic experts for all of the groups listed in their article.

Some other publications listing copepods found in ships in the Laurentian system include instances of, in our view, similar mischaracterizations of the native distributions and (or) taxonomy of certain species. We list the species of copepods found in the Great Lakes system that we consider to be nonindigenous (Table 1). For consistency, we adopted the definition of a nonindigenous species as "The condition of a species being moved beyond its natural range or natural zone of potential dispersal …" from the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 (Public Law 101-646, 16 USC 4701-4741, approved 29 November 1990). Our purpose here is to discuss only species considered to have been moved by human activities, rather than those that may have expanded their ranges naturally. Below, we discuss some species that have been mentioned in other publications and that present taxonomic or distributional problems. We have placed each of the species into categories for ease of classifying taxa in future studies of invasion biology (Table 2). A cryptogenic species is a species that is not demonstrably native or introduced (Carlton 1996).

Skistodiaptomus pallidus: occurs throughout the central and northeastern United States in ponds, lakes, and rivers. It has been recorded from Lakes Huron, Erie, St. Clair, and Ontario (Hudson and Lesko 2003), where it is considered as introduced by some (e.g., Mills et al. 1993). Individuals may occasionally be flushed from nearby stream–wetland complexes into the lakes proper, where they will likely not persist. Therefore, *S. pallidus* should be removed from the list of accidentally introduced species.

Acanthocyclops americanus: reported from ballast water by Locke et al. (1993), who termed it a potential invader. This taxon is not currently recognized as valid. It is a member of the controversial *vernalis–robustus* species complex, discussed below.

Acanthocyclops exilis: reported from ship hulls by Drake and Lodge (2007*b*) and is widespread in eastern North America, mainly in springs and small streams. Like *S. pallidus*, we consider it unlikely to become established in the Great Lakes proper.

Acanthocyclops robustus: the *robustus–vernalis* group remains incompletely understood (e.g., Dodson et al. 2003; Grishanin et al. 2006) and is so problematical from a morphological standpoint that it is difficult or impossible to ascertain whether old records or new collections represent a new introduction, without genetic analyses.

Table 2. Reasons for excluding copepod species from analyses of introductions.

Reason for exclusion	Copepod species
Cryptogenic species	*Acanthocyclops robustus*, *Eucyclops agilis*, *Eucyclops serrulatus*, *Onychocamptus mohammed*
Potential invader	*Bryocamptus pygmaeus*, *Canthocamptus staphylinus*, *Nitokra incerta*, *Thermocyclops crassus*
Nonindigenous to Great Lakes proper, but with natural dispersal mechanisms	*Cyclops strenuus*, *Skistodiaptomus pallidus*
Cannot become established (marine or estuarine species)	*Oithona similis* and other coastal or marine planktonic species
Unlikely to become established (different habitat requirements)	*Acanthocyclops exilis*, *Maraenobiotus insignipes*
Invalid taxon	*Acanthocyclops americanus*

Cyclops strenuus: supposedly a circumboreal species found in Alaska and northern Canada and has been collected rarely in Lake Superior. Holeck et al. (2004) included range extension and (or) natural dispersal among the possible modes of entry into the lake. Furthermore, North American records of *C. strenuus* may refer to the similar *Cyclops canadensis* (Hołyńska and Dahms 2004). We recommend removal of *C. strenuus* from the list of nonindigenous species.

Eucyclops agilis and *Eucyclops serrulatus*: in view of continuing revision of the *serrulatus* group (e.g., Alekseev et al. 2006), it is difficult to reliably assign morphs found outside Europe to one or another named species.

Megacyclops viridis: a Palaearctic species that was reported from Duluth Harbor in Lake Superior by Hudson et al. (1998). It is likely to have been introduced into that harbor, but the extent of its spread, if any, should be assessed.

Oithona similis: characterized as a "freshwater" species by Drake and Lodge (2007*b*); it is actually euryhaline–marine pelagic, unlikely to establish in the Great Lakes.

Thermocyclops crassus: reported from Lake Champlain by Duchovnay et al. (1992). Although this Palaearctic species has not yet been found in the Great Lakes proper, investigators should remain alert to its possible appearance.

Bryocamptus pygmaeus and *Canthocamptus staphylinus*: European harpacticoids that were reported from ballast water by Duggan et al. (2005). In spite of early records and inclusion in North American keys (e.g., Wilson and Yeatman 1959), we consider that both species are potential invaders.

Heteropsyllus nunni: native to estuaries of eastern North America (Hudson and Lesko 2003), not a Eurasian species as characterized by Grigorovich et al. (2003).

Nitokra incerta: reported from the Detroit River by Grigorovich et al. (2001). We are unaware of any reports since that time. Pending further field studies, we suggest that *N. incerta* be removed from the list of established nonindigenous species.

Onychocamptus mohammed: occurs on most continents, in estuaries or near-coastal fresh waters; it was collected in Lake Huron in 1974–1975 and since found in Lakes Erie, Huron, Ontario, and St. Clair (Hudson and Lesko 2003). Although it has been recorded from ballast water (Duggan et al. 2005; Johengen et al. 2005), its presence in the Great Lakes may well be the result of a natural range extension. Taking a conservative point of view, *O. mohammed* should be excluded from studies of human-mediated invasion, in agreement with Ricciardi (2006).

Salmincola lotae: a parasite of Palaearctic fishes, also recorded from burbot (*Lota lota*) in the Northwest Territories (Stewart and Bernier 1983, 1999) and in Lake Superior (Lasee et al. 1988). Although Hudson and Bowen (2002) suggested that the Lake Superior population might have been introduced, based on the above records we now consider that *S. lotae* occurs naturally in the Nearctic.

To date, more than 70 fresh- or brackish-water taxa of copepods have been recorded from ballast water, tank sediments, or hulls of ships in the Laurentian Great Lakes. Most of these were listed by Duggan et al. (2005), Johengen et al. (2005), or Drake and Lodge (2007*a*, 2007*b*). Species that are clearly not indigenous to the lakes include the following freshwater Palaearctic natives: *Acanthocyclops venustus*, *Cyclops abyssorum*, *Mesocyclops leuckarti*, *Paracyclops fimbriatus*, *Thermocyclops crassus*, *Thermocyclops oithonoides*, *Bryocamptus pygmaeus*, and *Canthocamptus staphylinus*; and the normally coastal brackish-water or euryhaline *Eurytemora affinis*, *Cyclopina littoralis*, *Ameira parvula*, *Halectinosoma curticorne*, *Mesochra pygmaea*, *Microarthridion littorale*, *Microsetella norwegica*, *Nitokra affinis*, *Nitokra hibernica*, *Schizopera baltica*, *Schizopera borutzkyi*, *Schizopera knabeni*, *Tachidius littoralis*, *Tisbe furcata*, and *Tisbe gracilis*. Native species found in the general region include *Epischura lacustris*, *Leptodiaptomus minutus*, *Leptodiaptomus siciloides*, *Senecella calanoides*, *Acanthocyclops brevispinosus*, *Diacyclops nanus*, *Diacyclops navus*, *Diacyclops nearcticus*, *Diacyclops thomasi*, *Eucyclops prionophorus*, *Macrocyclops albidus*, *Mesocyclops americanus*, *Mesocyclops edax*, *Microcyclops rubellus*, *Microcyclops varicans*, *Orthocyclops modestus*, *Paracyclops chiltoni*, *Tropocyclops prasinus*, *Bryocamptus zschokkei*, *Canthocamptus robertcokeri*, *Canthocamptus staphylinoides*, *Maraenobiotus insignipes*, *Mesochra alaskana*, *Nitokra lacustris*, *Nitokra spinipes, Onychocamptus mohammed*, and *Salmincola lotae*. Undetermined species that may or may not have been natives, some of which were reported by Harvey et al. (1999), include *Diaptomus* sp., *Eurytemora* sp., *Acanthocyclops* spp., *Cyclops* sp., *Diacyclops* sp., *Halicyclops* sp., *Mesocyclops* sp., *Paracyclops* sp., *Ameira* sp., *Maraenobiotus* sp., *Mesochra* sp., *Nitokra* spp., and *Schizopera* sp. Records of *Acanthocyclops americanus*, *Acanthocyclops exilis*, *Acanthocyclops robustus*, *Acanthocyclops vernalis*, *Cyclops strenuus*, *Eucyclops agilis*, *Eucyclops serrulatus*, *Megacyclops viridis*, *Oithona similis*, and *Salmincola lotae* present taxonomic or other problems, as discussed above.

In the study by Drake and Lodge (2007*a*) and some reports by others, the lack of familiarity of the authors or their

taxonomic consultants with the current literature on North American copepods is apparent. These flaws raise suspicion that taxonomic treatment of other groups may suffer from similar inadequacies. Although a single individual cannot be expected to be competent in all freshwater taxa, up-to-date regional keys now exist for copepods and some other zooplankton groups (e.g., Hudson and Lesko 2003; Aliberti et al. 2003).

In view of the current unstable taxonomy of copepods and many other groups of freshwater invertebrates, certain minimum criteria should be met in assessing whether a new record represents an introduction. First, the specimens must be examined by an experienced specialist. The likelihood of introduction should be evaluated based on the historical taxonomy and the species' known distribution and life-history characteristics, as exemplified by Mills et al. (1993) and Duggan et al. (2005), using the criteria for introduction proposed by Chapman and Carlton (1991). Second, voucher specimens should be deposited in a public institution. We have not located any reports on organisms found in ballast water that stated that voucher specimens were archived in permanent collections. Vouchers are the only means of verifying taxonomic determinations and also can provide a resource for further explorations of genetic differences that could assist in identifying the actual geographical origin of specimens. Third, to be considered as established, the species should be collected at least twice, from different localities or different time periods, with multiple life stages. Fourth, information on the species should be entered into an appropriate website, with illustrations and information on identification, distribution, life history, ecology, and taxonomic synonyms.

No one disputes that many nonindigenous aquatic vertebrates, invertebrates, and plants have invaded the Laurentian system, but because of low densities, they are not detected, recognized, or do not persist. Our concern is that organisms should be examined by experienced taxonomists. We hope that careful procedures will improve the accuracy of estimates of the seriousness of the transport problem and the means to deal with it.

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References

Alekseev, V., Dumont, H.J., Pensaert, J., Baribwegure, D., and Vanfleteren, J.R. 2006. A redescription of *Eucyclops serrulatus* (Fischer, 1851) (Crustacea: Copepoda: Cyclopoida) and some related taxa, with a phylogeny of the *E. serrulatus*-group. Zool. Scr. **35**: 123–147.

Aliberti, M.A., Bauer, D.J., Bradt, S.R., Carlson, B., Carlson, S.C., Godkin, W.T., Greene, S., Haney, J.F., Kaplan, A., Melillo, S., Smith (Nowak), J.L., Ortman, B., Quist, J.E., Reed, S., Rowin, T., and Stemberger, R.S. 2003. An image-based key to the zooplankton of the northeast (USA). Version 2.0 [online]. Center for Freshwater Biology, University of New Hampshire, Durham, N.H. Available from cfb.unh.edu/CFBkey/index.html [accessed 18 May 2007].

Carlton, J.T. 1996. Biological invasions and cryptogenic species. Ecology, **77**: 1653–1655.

Chapman, J.W., and Carlton, J.T. 1991. A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). J. Crustac. Biol. **11**: 386–400.

Dodson, S.I., Grishanin, A.K., Gross, K., and Wyngaard, G.A. 2003. Morphological analysis of some cryptic species in the *Acanthocyclops vernalis* species complex from North America. Hydrobiologia, **500**: 131–143.

Drake, J.M., and Lodge, D.M. 2007*a*. Rate of species introductions in the Great Lakes via ships' ballast water and sediments. Can. J. Fish. Aquat. Sci. **64**: 530–538.

Drake, J.M., and Lodge, D.M. 2007*b*. Hull fouling is a risk factor for intercontinental species exchange in aquatic ecosystems. Aquat. Invasions, **2**: 121–131.

Duchovnay, A., Reid, J.W., and McIntosh, A. 1992. *Thermocyclops crassus* (Crustacea: Copepoda) present in North America: a new record from Lake Champlain. J. Gt. Lakes Res. **18**: 415–419.

Duggan, I.C., van Overdijk, C.D.A., Bailey, S.A., Jenkins, P.T., Limén, H., and MacIsaac, H.J. 2005. Invertebrates associated with residual ballast water and sediments of cargo-carrying ships entering the Great Lakes. Can. J. Fish. Aquat. Sci. **62**: 2463–2474.

Great Lakes Environmental Research Laboratory (GLERL). 2006. Great Lakes aquatic nonindigenous species list [online]. NOAA National Center for Research on Aquatic Invasive Species, GLERL, and Cooperative Institute for Limnology and Ecosystems Research, University of Michigan, Ann Arbor, Mich. Available from www.glerl.noaa.gov/res/Programs/invasive/ [accessed 10 May 2007].

Grigorovich, I.A., Dovgal, I.V., MacIsaac, H.J., and Monchenko, V.I. 2001. *Acineta nitocrae*: a new suctorian epizooic on nonindigenous harpacticoid copepods, *Nitocra hibernica* and *N. incerta*, in the Laurentian Great Lakes. Arch. Hydrobiol. **152**: 161–176.

Grigorovich, I.A., Colautti, R., Mills, E.L., Holeck, K., Ballert, A., and MacIsaac, H.J. 2003. Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Can. J. Fish. Aquat. Sci. **60**: 740–756.

Grishanin, A.K., Rasch, E.M., Dodson, S.I., and Wyngaard, G.A. 2006. Genetic architecture of the cryptic species complex of *Acanthocyclops vernalis* (Crustacea: Copepoda). II. Crossbreeding experiments, cytogenetics, and a model of chromosomal evolution. Evolution, **60**: 247–256.

Harvey, M., Gilbert, M., Gauthier, D., and Reid, D.M. 1999. A preliminary assessment of risks for the ballast water-mediated introduction of nonindigenous marine organisms in the Estuary and Gulf of St. Lawrence. Can. Tech. Rep. Fish. Aquat. Sci. 2268.

Holeck, K.T., Mills, E.L., MacIsaac, H.J., Dochoda, M.R., Colautti, R.J., and Ricciardi, A. 2004. Bridging troubled waters: biological invasions, transoceanic shipping, and the Laurentian Great Lakes. Bioscience, **54**: 919–929.

Hołyńska, M., and Dahms, H.-U. 2004. New diagnostic microcharacters of the cephalothoracic appendages in *Cyclops* O.F. Müller, 1776 (Crustacea, Copepoda, Cyclopoida). Zoosystema, **26**: 175–198.

Hudson, P.L., and Bowen, C.A., II. 2002. First record of *Neoergasilus japonicus* (Poecilostomatoida: Ergasilidae), a parasitic copepod new to the Laurentian Great Lakes. J. Parasitol. **88**: 657–663.

Hudson, P.L., and Lesko, L.T. 2003. Free-living and parasitic copepods (including branchiurans) of the Laurentian Great Lakes:

keys and details on individual species [online]. Great Lakes Science Center, Ann Arbor, Mich. Available from www.glsc.usgs.gov/greatlakescopepods/ [accessed 21 May 2007].

Hudson, P.L., Reid, J.W., Lesko, L.T., and Selgeby, J.H. 1998. Cyclopoid and harpacticoid copepods of the Laurentian Great Lakes. Bull. Ohio Biol. Surv. **12**(2): 1–50.

Johengen, T., Reid, D., Fahnenstiel, G., MacIsaac, H., Dobbs, F., Doblin, M., Ruiz, G., and Jenkins, P. 2005. Assessment of transoceanic NOBOB vessels and low-salinity ballast water as vectors for non-indigenous species introductions to the Great Lakes. Final Report. Cooperative Institute for Limnology and Ecosystems Research, School of Natural Resources and Environment, University of Michigan; and NOAA-Great Lakes Environmental Research Laboratory, Ann Arbor, Mich.

Lasee, B.A., Sutherland, D.R., and Moubry, M.E. 1988. Host–parasite relationships between burbot (*Lota lota*) and adult *Salmincola lotae* (Copepoda). Can. J. Zool. **66**: 2459–2463.

Locke, A., Reid, D.M., van Leeuwen, 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.

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. Gt. Lakes Res. **19**: 1–54.

Ricciardi, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Divers. Distrib. **12**: 425–433.

Stewart, D.B., and Bernier, L.M.J. 1983. An aquatic resource survey of King William and Victoria Islands, and the northeastern District of Keewatin, Northwest Territories. Lands Directorate of Environment Canada, Ottawa, Ont., and Northern Environment Directorate of Indian and Northern Affairs, Ottawa, Ont. Background Rep. No. 3.

Stewart, D.B., and Bernier, L.M.J. 1999. Common parasites, diseases and injuries of freshwater fishes in the Northwest Territories and Nunavut. Prepared by Arctic Biological Consultants for Fisheries and Oceans Canada, Central and Arctic Region, Winnipeg, Man.

Wilson, M.S., and Yeatman, H.C. 1959. Free-living Copepoda. *In* Freshwater biology. 2nd ed. *Edited by* W.T. Edmondson. Wiley, New York. pp. 735–868.