Journal of Great Lakes Research 39 (2013) 622–629

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Lakewide dominance does not predict the potential for spread of dreissenids

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ARTICLE INFO

Article history:
Received 18 March 2013
Accepted 29 August 2013
Available online 5 October 2013

Communicated by Michael Sierszen

Index words:
Dreissena polymorpha
Dreissena rostriformis bugensis
Vectors of spread
Recreational boats
Invasive species
Great Lakes

ABSTRACT

In recent years, quagga mussels (*Dreissena rostriformis bugensis*) have almost completely replaced zebra mussels (*Dreissena polymorpha*) in the Lower Great Lakes. As recreational boats are the main vector of spread for dreissenids in North America, this study examined whether lakes Erie and Ontario could still be sources for the spread of zebra mussels. In the summer–fall of 2010, the abundance of each species of *Dreissena* on 196 boats from 5 marinas in lakes Erie and Ontario was examined. Additional samples of *Dreissena* in 2010–2012 were collected in tributaries, bays, and in the upper littoral zones of these lakes. A total of 77 boats were fouled by *Dreissena*, and of those 61 were fouled by both species, 13 were fouled just by zebra mussels, and only 3 were fouled solely by quagga mussels. Although quagga mussels compose ~99% of dreissenids in eastern Lake Erie and in Lake Ontario, on boats at most marinas sampled, zebra mussels were usually more abundant and significantly larger than quagga mussels. Refugia for zebra mussels were found in bays, tributaries, and upper littoral zones with high wave activity. Thus, although quagga mussels are now more abundant than zebra mussels within the Lower Great Lakes, these waterbodies still have the potential to be a source for the spread of zebra mussels, and for some vectors, the propagule pressure from zebra mussels is likely greater than that from quagga mussels.

Introduction

Over the past century there has been an exponential increase in the transport of nonnative species, which then become of concern in the new aquatic habitats they invade (Leppäkoski and Olenin, 2000; Ruiz and Carlton, 2003). In North America, at least 182 nonnative species have been introduced to the Great Lakes over the last 150 years, more than any other freshwater system in North America (Ricciardi, 2006). Being the major port of entry for freshwater aquatic invaders, these waterbodies then act as a major source for their spread to inland waterbodies across North America (Padilla et al., 1996). Although some of these species may be closely related, the environmental and economic impacts, even for congeners, may differ (Karatayev et al., 2011, 2013). Therefore, contrasting congeners with different rates of spread at different spatial scales may be a useful tool for predicting which invaders will be more successful at spreading across space and time, especially for different vectors and mechanisms of spread (Karatayev et al., 2011, 2013).

The zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostriformis bugensis*) are among the most prominent aquatic invaders in North America. In Lake Erie, *D. polymorpha* was first discovered in 1986 (Carlton, 2008), and *D. r. bugensis* was first found in 1989 (Mills et al., 1993). Both species have planktonic larvae and an attached adult stage, representing a novel ecological type for North American freshwaters. They act as ecosystem engineers and have large ecological and economic impacts (reviewed in Karatayev et al., 1997, 2002, 2007; Nalepa and Schloesser, 1993; O'Neill, 2008). Although the importance of different vectors for the introduction and spread of dreissenids has varied widely over the last two centuries (reviewed in Karatayev et al., 2007, 2011), recreational boating is currently the major vector of spread from the initial site of introduction (Lake Erie) for these invaders in North America (Johnson and Carlton, 1996; Johnson and Padilla, 1996; Johnson et al., 2001, 2006; Padilla et al., 1996). Given the extensive use of the Great Lakes by recreational boaters, these waterbodies have become the major sources for the spread of *Dreissena* in the region.

Initially, lakes Erie and Ontario were dominated by *D. polymorpha*, which achieved high densities in the littoral zones, while *D. r. bugensis* was found in the deep areas of the lakes (Dermott and Dow, 2008; Patterson et al., 2005; Watkins et al., 2007). However, in the mid-1990s, the zebra mussel was displaced by quagga mussels, and by the mid-2000s quagga mussels composed >90% of dreissenids in both lakes (Patterson et al., 2005; Pennuto et al., 2012; Watkins et al.,

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http://dx.doi.org/10.1016/j.jglr.2013.09.007

2007). Although the Lower Great Lakes have become dominated by *D. r. bugensis* and its recent spread to lakes in the western U.S. has garnered a great deal of attention (Karatayev et al., 2012; Wong et al., 2012), *D. polymorpha* has maintained a higher rate of spread than *D. r. bugensis* over the entire history of their invasion of U.S. waterbodies. By 2008, zebra mussels had colonized twice as many states, almost eight times more counties, and over 15 times more waterbodies than quagga mussels (Karatayev et al., 2011).

Since their invasion of North America, a number of studies have focused on the spread of dreissenids on trailered boats (usually remaining in the water for 1–4 days and stored on a trailer when not used) to inland waterbodies in the Great Lakes Region (e.g., Bossenbroek et al., 2007; Johnson et al., 2001, 2006; Padilla et al., 1996). These studies either did not include or did not focus on the 'resident boats' (20–50 ft long and remain in the water for >3 months) of infested waterbodies, because the movement of these boats to other waterbodies was far less than for other types of boats. However, resident boats, which spend many months in infested waterbodies, may be colonized to a much greater degree, and may therefore introduce more *Dreissena* per boat when moved than transient boats (Bossenbroek et al., 2007; Johnson et al., 2001, 2006). Such direct hull fouling can be an important vector for the spread of aquatic non-indigenous species in both marine and freshwater environments (Ashton et al., 2006; Floerl et al., 2005). In North American freshwaters, hull fouling may be most extensive within the Great Lakes, where many marinas are sheltered from waves by breakwaters. Floerl and Inglis (2003) found that such marinas experience notably lower water velocities compared to "open" marinas, which could enhance the colonization of boats by *Dreissena* larvae. This vector is of particular importance given the high population density and large number of such boats in the Great Lakes. Out of almost 4.3 million recreational boats in the eight Great Lakes states (a third of all U.S. recreational vessels), about 107,000 boats were kept in Great Lakes county marinas during the boating season of 2003 (Great Lakes Recreational Boating, 2008). In a recent study, Brown and Stepien (2010) used DNA evidence to suggest that the invasion of *Dreissena* into the western U.S. originated from the eastern Great Lakes, and large boats were the most likely vectors (Benson et al., 2012).

We examined resident boats that remained in the water throughout the whole boating season (usually May–September), which can be heavily fouled by *Dreissena* (Bossenbroek et al., 2007; Johnson et al., 2001). The main objectives of this study were to: (1) determine the relative abundance of zebra mussels and quagga mussels on boats in marinas in the Lower Great Lakes and (2) identify possible refuges for zebra mussels in these lakes.

Methods

A total of 196 boats were examined for dreissenid infestation at 5 marinas in New York State, including three marinas on Lake Erie and two marinas on Lake Ontario (Fig. 1). With the exception of Olson Marina, samples from marinas were collected between August 14 and 20, 2010 (Table 1). Marinas within 60 km of Buffalo, NY, were selected based on the presence of large resident boats (20–50 ft long) and permission from marina owners. All marinas examined were enclosed by breakwaters and had only narrow outlets to open water. In addition, the marinas on Lake Ontario were situated at the mouths of inflowing tributaries and bays. Sampled boats included power boats, which usually had large outboard motors, numerous crevices, and/or hull irregularities. For all samples collected, mussels were identified to species, and shell length was measured with calipers to the nearest 0.1 mm.

When possible, we collected samples within each marina from: 1) resident power and sailboats, 2) permanent artificial or natural substrates, and 3) temporary substrates (usually floating docks). In addition, we surveyed permanent substrates in the upper littoral zones, lower reaches of tributaries, and additional marinas to determine whether any of these locations had refuge populations of zebra mussels (Table 1, Fig. 1).

Boat sampling

At each marina, at least 30 boats (or all boats if <30 were available) were examined by snorkeling (Table 1). All boats sampled were moored at dockings rented for the entire summer, and almost all had been placed in the water between April and June of 2010. Boats were sampled

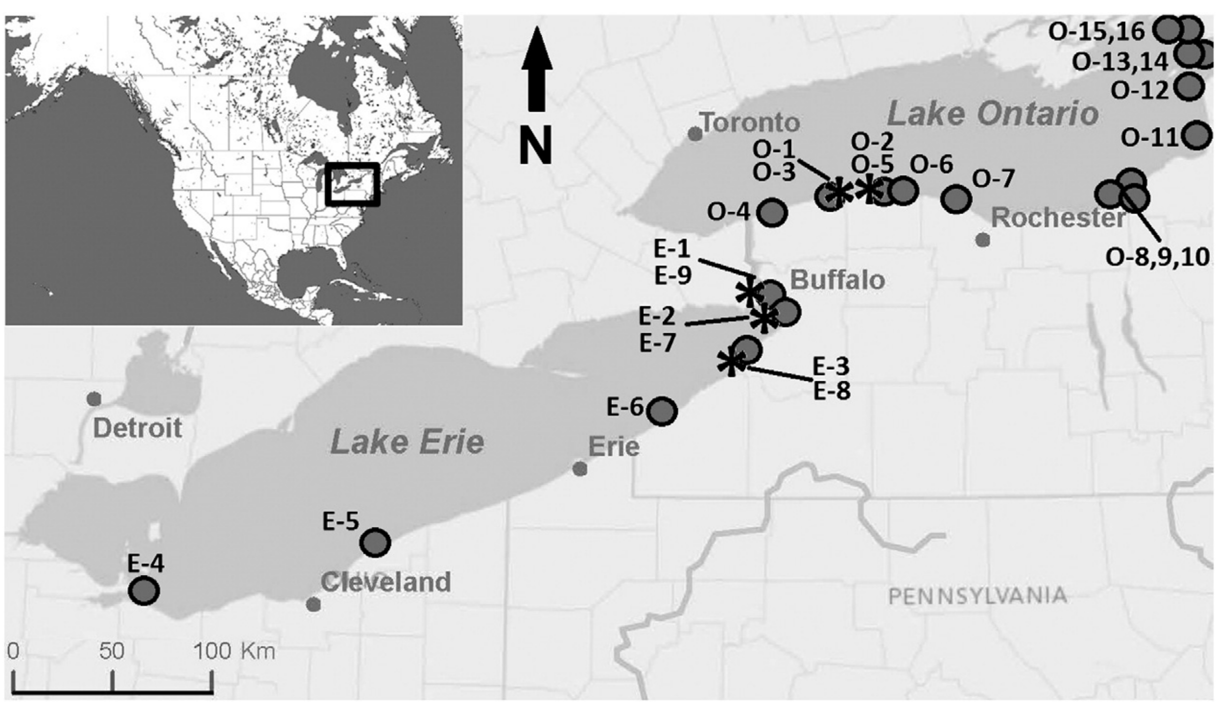

Fig. 1. Locations of sampling sites on the Lower Great Lakes. Asterisks represent marinas where boats and (where available) temporary and/or permanent substrates were sampled. Shaded circles represent samples of dreissenids collected in tributaries, bays, marinas, or in the upper littoral zone. For site names and sampling details, see Table 1.

systematically at each marina. Because the marinas did not cover a large area (<20,000 m^2) and boats were not grouped by type or size, we assumed that our samples represented a random selection of boats at each marina. The only exception was Olson Marina, within the city of Buffalo, which specialized in "winterizing" boats (i.e., removing, cleaning, and storing boats for the offseason). At this marina, we examined infested boats that had been removed from the water but not yet cleaned of dreissenids. By verifying with marina workers, we sampled boats that were removed in September 2010 from the nearby Buffalo NFTA Boat Harbor (where we were not permitted to sample). All boats were examined for dreissenids, with special attention paid to irregular sections and motors, and all *Dreissena* found were collected. In the very few cases when mussel infestation was too extensive to count all attached dreissenids on a boat, mussels from at least 5 random subsamples (20 × 20 cm) were scraped from the boat and placed into closable plastic bags. The total number of dreissenids per boat was then estimated by using the sampled density and the whole infested area of the boat.

Table 1
Sampling locations for *Dreissena polymorpha* and *D. rostriformis bugensis* in the Lower Great Lakes. Site number (E — Lake Erie; O — Lake Ontario) corresponds to sites in Fig. 1.

Site number	Sites	Coordinates	Sample size	Sampling date
Lake Erie, marinas				
E-1	Buffalo Yacht Club Marina:	42°53′50″N,		8/14/10
	Power boats	78°54′05″W	16	
	Sail boats		15	
	Floating docks		3	
E-2	Olson Marina:	42°52′54″N, 78°53′12″W		10/8/10–10/10/10
	Power boats[a]		21	
	Floating docks		3	
E-3	Sturgeon Point Marina:	42°41′30″N,		
	Power boats	79°02′45″W	54	8/19/10
	Power boats[a]		40	9/09/10
	Floating docks		3	8/19/10
Lake Erie, permanent substrates				
E-4	Monroeville Marina	41°26′49″N, 82°40′27″W	1	6/08/11
E-5	Fairfield Marina	41°45′34″N, 81°16′38″W	5	6/09/11
E-6	Westfield Marina	42°20′33″N, 79°35′37″W	2	6/15/11
E-7	Buffalo River	42°52′20″N, 78°52′26″W	4	6/15/11
E-8	Wendt Park Beach wavebreaker	42°41′01″N, 79°03′07″W	3	8/19/10
E-9	Black Rock Canal	42°53′56″N, 78°54′07″W	2	8/14/10
Lake Ontario, marinas				
O-1	Newfane Marina:	43°18′50″N,		8/20/10
	Power boats	78°50′34″W	13	
	Sail boats		5	
	Permanent substrates		6	
O-2	Sunset Marina:	43°20′10″N,		8/20/10
	Power boats	78°42′58″W	22	
	Sail boats		10	
	Floating docks		3	
	Permanent substrates		3	
Lake Ontario, permanent substrates				
O-3	Wavebreaker near Wilson, NY	43°19′09″N, 78°49′34″W	3	8/20/10
O-4	Branches in Fourmile Creek State Park	43°16′36″N, 78°59′53″W	3	8/07/12
O-5	Littoral rocks near Golden Hill State Park	43°22′14″N, 78°28′18″W	3	8/04/12
O-6	Rocks in mouth of Johnson Creek	43°22′17″N, 78°15′54″W	4	8/02/12
O-7	Littoral rocks in Braddock Bay	43°19′10″N, 77°42′49″W	3	7/31/12
O-8	Littoral rocks in The Pond near Fair Haven, NY	43°20′34″N, 76°41′55″W	1	7/18/12
O-9	Littoral rocks in Little Sodus Bay near Fair Haven, NY	43°20′30″N, 76°42′9″W	1	7/19/12
O-10	Littoral rocks in Blind Sodus Bay near Fair Haven, NY	43°20′10″N, 76°44′2″W	1	7/19/12
O-11	Littoral rocks in South Pond near Sandy Creek, NY	43°37′32″N, 76°11′45″W	1	7/21/12
O-12	Littoral rocks in Benns Cove	43°53′19″N, 76°8′45″W	1	7/25/12
O-13	Littoral rocks in Black River Bay	43°58′35″N, 76°4′39″W	1	7/24/12
O-14	Littoral rocks in Black River Bay west of Dexter, NY	43°59′33″N, 76°5′19″W	1	7/24/12
O-15	Littoral rocks in Chaumont Bay, Long Point State Park	44°1′41″N, 76°12′59″W	1	7/25/12
O-16	Littoral rocks in Chaumont Bay, boat launch	44°4′5″N, 76°8′57″W	1	7/25/12

[a] Only infested boats were examined.

Boat infestation rate (the proportion of examined boats fouled by *Dreissena*, multiplied by 100) was calculated for each of 4 marinas (135 boats in total). Data collected from Olson Marina and Sturgeon Point Marina in September were excluded from the analysis of the proportion of infested boats because we were unable to obtain a random sample of the boats and examined only infested boats. However, these data were included in the analysis of the relative abundance and size–frequency distribution of dreissenid species on infested boats.

Temporary and permanent substrates in marinas

On the same day that boats were sampled for *Dreissena*, we sampled temporary and permanent substrates in the marinas whenever possible (Table 1). Samples of temporary substrates (present only during the boating season and colonized with only young-of-the-year dreissenids) included floating docks which were winterized each fall. To examine the multi-year *Dreissena* populations within the marinas, we sampled permanent substrates (present year-round), including concrete walls, rocks, and pillars. Several samples were collected from each source by scraping and collecting at least ~200 dreissenids whenever possible.

Potential zebra mussel refugia in lakes

After finding that zebra mussels frequently dominate the dreissenids found on sampled boats in eastern Lake Erie and Lake Ontario, in contrast to the benthic environment where quagga mussels constituted ~99% of all dreissenids (Karatayev et al., 2011, in review; Pennuto et al., 2012), we attempted to locate possible refuges for *D. polymorpha*. We sampled permanent substrates in the mouths of inflowing tributaries, bays, and marinas in lakes Erie and Ontario (Table 1, Fig. 1). When dreissenids were present, we collected 3 to 5 (20 × 20 cm) random samples of *Dreissena* using the same method as for sampling substrates inside marinas described above.

Statistical analysis

The size–frequency distribution and relative abundance of each species of *Dreissena* were determined for each sample collected. To determine the infestation intensity of boats in each marina, we calculated the mean number of dreissenids on each infested boat. To compare the average size of *D. r. bugensis* and *D. polymorpha*, we used a two-sided Welch modification of the *t*-test (for samples with unequal variances, Zar, 1996). We used a non-parametric alternative to the *t*-test, the Mann–Whitney *U* test (Zar, 1996), to compare the proportion of *D. polymorpha* between substrate types and locations. For all statistical tests, Statistica software (STATISTICA data analysis software system, version 8.0, StatSoft, Inc. 2007, www.statsoft.com) was used. Effects were considered statistically significant at $p < 0.05$. When multiple tests were conducted on the same data, we used a sequential Bonferroni correction to adjust the critical alpha considered for statistical significance (Rice, 1989). Where appropriate, we present the critical alpha (α) with the results of each statistical test.

Results

Boat infestation

Out of 135 boats at 4 marinas sampled, 34.1% were infested with at least one species of *Dreissena*. The two marinas on Lake Erie (Buffalo Yacht Club and Sturgeon Point) had a lower infestation rate (20.4%) than those on Lake Ontario (48.8%) (Table 2). Sailboat infestation rate was less than that of power boats (20.0% vs. 42.4%). In contrast to the marinas on Lake Erie, *D. polymorpha* was present on all infested boats from Lake Ontario and was the dominant species (Table 2).

An additional 21 boats were sampled at Olson Marina, all of which had mussels attached. Of these boats, 20 had both species, and 1 had just quagga mussels. Overall, of the 77 boats with mussels attached, 61 (79.2%) were fouled by both species, 13 (16.9%) were fouled by zebra mussels only, and only 3 boats (3.9%) were fouled by just quagga mussels. The relative abundance of *D. polymorpha* on boats in Lake Erie varied among marinas, but was higher on infested boats than on temporary substrates (floating docks) (Fig. 2, Table 2, $U = 148.5$, $Z = 2.76$, $p = 0.006$, critical $\alpha = 0.05$, Mann–Whitney *U* test). Similarly, in Sunset Marina on Lake Ontario, the only marina where we were able to collect samples from both temporary and permanent substrates, the relative abundance of *D. polymorpha* was greater on temporary than on permanent substrates.

We found that the relative abundance of zebra mussels on boats kept in marinas at the mouths of tributaries (Newfane Marina on Eighteen Mile Creek and Sunset Marina on East Branch of Twelve Mile Creek) was significantly greater than that on boats kept in marinas not on inflowing tributaries (Sturgeon Point Marina, Olson Marina, and the Buffalo Yacht Club) ($U \ll 0.001$, $Z = -6.5$, $p \ll 0.001$, critical $\alpha = 0.025$, Mann–Whitney *U* test).

Size–frequency distribution

On boats at the 4 marinas sampled, *D. polymorpha* were significantly larger than *D. r. bugensis* ($p < 0.01$, *t*-test, Table 4). The only exception was the Olson Marina, where *D. r. bugensis* was significantly larger ($p = 0.004$, *t*-test). In addition, the largest individuals on each boat at all marinas were always *D. polymorpha*, even at the Olson Marina. However, this pattern was not evident when all data were pooled across all marinas within each lake (Fig. 2) because our sampling spanned several months during the dreissenid growing season (animals sampled later in the season were larger than those sampled earlier) and there were large environmental differences between marinas.

On floating docks, *D. polymorpha* were significantly larger than *D. r. bugensis* at the Sunset Bay Marina ($p < 0.001$, *t*-test, Table 4). There were too few zebra mussels on floating docks in marinas on

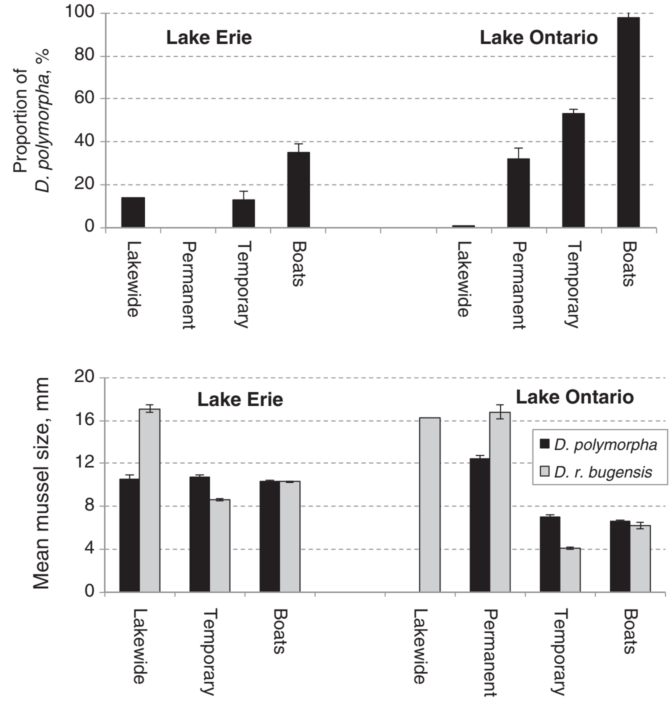

Fig. 2. Proportion of *Dreissena polymorpha* (%, average ± standard error) from total number of dreissenids (upper panel) and mean size of *Dreissena* by species found lakewide and on different types of substrates in marinas on lakes Erie and Ontario where boats were sampled (lower panel). Note: permanent substrates were not available in the Lake Erie marinas; marina samples from Lake Ontario are given for Sunset marina, where all 3 substrate types were available. Lakewide data for Lake Erie from Karatayev et al. (in review), Lake Ontario from Pennuto et al. (2012); no data were available for mean size of Lake Ontario *D. polymorpha*.

Lake Erie to find a similar significance, but each sample showed a similar trend, and *D. polymorpha* was significantly larger than *D. r. bugensis* when these samples of temporary substrates were pooled ($p < 0.001$, *t*-test, Fig. 2). In contrast, *D. r. bugensis* had a larger mean size than *D. polymorpha* on permanent substrates in Sunset Bay Marina ($p < 0.001$, *t*-test, Fig. 2).

Boat infestation intensity

The number of dreissenids attached to boats was low in both lakes and usually did not exceed a few hundred mussels per infested boat (Table 5). Most dreissenids were found in crevices on the hull or engine and only occasionally on the boat hull. The highest number of dreissenids (117,000 zebra mussels, 886,000 quagga mussels; 1,003,000 mussels total) was found on a boat removed from the Buffalo NFTA Boat Harbor for winterizing; this boat was not operated

Table 2
Infestation of boats with dreissenids (% infested from total examined) and relative abundance of *Dreissena polymorpha* (% of total dreissenids) on boats and substrates in marinas in the Lower Great Lakes (mean ± standard error, sample size in parenthesis).

Marina	Boats			Temporary substrates
	Infested with either species, %	Infested with *D. polymorpha*, %	Relative abundance of *D. polymorpha*, %	Relative abundance of *D. polymorpha*, %
Lake Erie				
Buffalo Yacht Club	12.9 (31)	6.5	13.6 ± 11.6	0.7 ± 0.3 (3)
Sturgeon Point	31.5 (54)	31.5	61.7 ± 4.9	19.9 ± 6.5 (3)
Olson	–	–	26.4 ± 3.2	18.9 ± 2.8 (3)
Average	22.2	19.0	33.8	13.2
Lake Ontario				
Sunset	53.1 (32)	53.1	98.4 ± 0.6	52.6 ± 1.7 (3)
Newfane	44.4 (18)	44.4	98.6 ± 0.9	–
Average	48.8	48.8	98.5	52.6

Table 3
Relative abundance (%), mean sizes (± standard errors), and sample size (*n*) of *Dreissena polymorpha* and *D. rostriformis bugensis* on permanent substrates in the littoral areas, marinas, and tributaries of lakes Erie and Ontario. Note: at some sites, only one sample was collected, and therefore no standard error for the proportion of *D. polymorpha* is given.

Location	Relative abundance of *D. polymorpha*, %	Length, mm				
		D. polymorpha		*D. r. bugensis*		*p*-Value
		Length	*n*	Length	*n*	
Lake Erie						
Monroeville Marina	13.0	12.4 ± 0.9*	48	9.0 ± 0.2	320	<0.001
Fairfield Marina	63.7 ± 3.2	13.2 ± 0.1	523	13.0 ± 0.3	264	0.379
Westfield Marina	16.5 ± 1.5	10.7 ± 0.6	74	12.8 ± 0.2*	376	<0.001
Buffalo River bottom samples	73.1 ± 17.5	14.4 ± 0.2	263	18.0 ± 0.7*	53	<0.001
Wendt Park wavebreaker	78.2 ± 21.8	14.2 ± 0.2	141	19.5 ± 0.5*	64	<0.001
Littoral rocks in Black Rock Canal	13.8 ± 6.5	9.1 ± 0.6*	24	7.0 ± 0.3	194	0.001
Lake Ontario						
Sunset Bay Marina	31.9 ± 5.2	4.1 ± 0.2	94	16.5 ± 0.7*	168	<0.001
Newfane Marina	90.8 ± 3.7	13.9 ± 0.3	526	17.8 ± 1.4*	56	0.008
Wavebreaker near Wilson, NY	3.1 ± 1.2	21.6 ± 2.1*	8	11.9 ± 0.4	267	0.002
Littoral rocks in The Pond near Fair Haven, NY	35.0	17.1 ± 0.5	21	16.4 ± 0.3	39	0.271
Littoral rocks in Little Sodus Bay	10.6	15.3 ± 0.5	17	21.9 ± 0.5*	143	<0.001
Littoral rocks in Blind Sodus Bay	6.0	12.9 ± 1.6	6	12.6 ± 0.2	94	0.869
Littoral rocks in South Pond near Sandy Creek, NY	100.0	18.7 ± 0.8	42		0	
Littoral rocks in Black River Bay	96.9	14.6 ± 0.2	124	13.9 ± 0.4	4	0.176
Littoral rocks in Black River Bay, west of Dexter, NY	45.9	15.8 ± 0.3	39	16.8 ± 0.5	46	0.141
Littoral rocks in Benns Cove	8.8	12.4 ± 0.9	8	16.1 ± 0.5*	83	0.005
Littoral rocks in Chaumont Bay, Long Point State Park	11.3	17.2 ± 1.1	12	20.2 ± 0.4*	94	0.020
Littoral rocks in Chaumont Bay, boat launch	83.5	17.0 ± 0.5	86	20.7 ± 1.1*	17	0.004
Littoral rocks in Braddock Bay	30.0 ± 17.5	12.1 ± 0.7*	25	4.9 ± 0.4	98	<0.001
Rocks in mouth of Johnson Creek	44.0 ± 6.9	24.5 ± 0.5	58	27.0 ± 0.5*	83	<0.001
Littoral rocks near Golden Hill State Park	47.0 ± 13.6	9.8 ± 0.3	54	10.4 ± 0.3	52	0.218
Branches in Fourmile Creek State Park	68.0 ± 7.1	18.5 ± 0.2	122	19.6 ± 0.3*	59	0.003

* Significantly larger ($p < 0.05$, *t*-test) size.

during the 2010 summer season and was excluded from the analysis. Among the marinas, the lowest average number of dreissenids attached to infested boats was in Newfane Marina and the highest in Olson Marina (Table 5). The high average number of dreissenids per boat in Olson Marina was due, in part, to the presence of a few heavily infested boats (3 boats had ~2400–2800 *D. r. bugensis* each, and 2 of these also had ~1000 *D. polymorpha*).

Refuges for zebra mussels in the Lower Great Lakes

We found *D. polymorpha* refugia with permanent (multi-year) populations of zebra mussels on breakwaters in the upper littoral zone, tributaries, bays, and marinas of the Lower Great Lakes (summarized in Tables 1 and 3). The proportion of *D. polymorpha* in these refugia varied greatly, from 6 to 100% of all dreissenids (Table 3). There was no significant difference in the relative abundance of *D. polymorpha* between these lakes when all permanent substrates were pooled ($U = 258.5$, $Z = 0.60$, $p = 0.55$, Mann–Whitney *U* test). The mean dreissenid size also varied across refugia; however, in Lake Ontario, *D. r. bugensis* was significantly larger than *D. polymorpha* at over half (9 out of 16) of the sampled locations (Table 3).

Discussion

Zebra mussel presence and refugia in the Lower Great Lakes

Both *D. polymorpha* and *D. r. bugensis* were introduced into the Lower Great Lakes in the late-1980s. Initially zebra mussels dominated these lakes, which became the major source for the invasion of *D. polymorpha* in North American lakes (Johnson et al., 2006; Padilla et al., 1996). In the mid-1990s, *D. r. bugensis* began to increase in abundance in lakes Erie and Ontario, especially in deep waters (Dermott and Dow, 2008; Patterson et al., 2005; Watkins et al., 2007). Through time, quagga mussels gradually replaced the zebra mussels in these lakes and are now dominant (Karatayev et al., 2011; Mills et al., 1999; Nalepa et al., 2010; Patterson et al., 2005). By 2002, 92% of the dreissenids in Lake Erie were quagga mussels, and zebra mussels were abundant only in the shallower western basin (Patterson et al., 2005). By 2009–2012, 99% of the mussels in benthic surveys were quaggas in the eastern basin and 67% in the western basin (Karatayev et al., in review). A similar pattern was seen in Lake Ontario, where the proportion of quagga mussels increased to 93% by 1999 and to 99% by 2003 (Watkins et al., 2007). Extensive sampling of Lake Ontario from 2 to 20 m depth in 2008 found that 99% of all dreissenids in the nearshore areas were quagga mussels (Pennuto et al., 2012).

We found that in contrast to the benthic environment, zebra mussels were present on virtually all boats fouled with *Dreissena*. All sampled boats in lakes Erie and Ontario were deployed free of dreissenids at the beginning of the navigation season, and by the time of our sampling in the fall, the boats were colonized by young-of-the-year dreissenids. While the relative abundance of zebra mussels on boats in sampled Lake Erie marinas varied from 14 to 62% of all dreissenids, in Lake Ontario, where almost no zebra mussels were found in the benthic habitats, 98% of all dreissenids found on boats in both of the marinas that were sampled were *D. polymorpha*.

The relative abundance of zebra mussels in marinas varied widely, suggesting that the likely sources of *D. polymorpha* larvae also differed among marinas. Refugia for zebra mussels in these lakes include tributaries, bays, and possibly shallow areas of the lakes with greater water motion (e.g., breakwaters), which generally are not sampled during routine benthic surveys. Large bays and wetlands adjacent to lakes Erie and Ontario are generally shallow and eutrophic and have high seston concentrations due to the inflowing tributaries. Such habitats are better environments for zebra mussels than open lakes, where quagga mussels form high densities in the profundal zone and have greater survivorship than zebra mussels when food concentrations are low (reviewed in Karatayev et al., 2013, 2011). These bays and wetlands are environmentally very similar to the Dnieper River Delta and Dnieper–Bug Liman (Ukraine), where both dreissenid species co-occur (reviewed in Karatayev et al., 2011). Vegetation in wetlands lowers the rate of veliger dispersal in these ecosystems (Bodamer and

Table 4
Mean length (mm ± standard error) and sample size (n) of *Dreissena polymorpha* and *D. rostriformis bugensis* on boats and temporary substrates from lakes Erie and Ontario marinas.

Marina	Boats					Temporary substrates				
	D. polymorpha		*D. r. bugensis*		p-Value	*D. polymorpha*		*D. r. bugensis*		p-Value
	Length	n	Length	n		Length	n	Length	n	
Lake Erie										
Buffalo Yacht Club	8.7 ± 0.7*	25	5.2 ± 0.1	241	<0.001	6.3 ± 1.3	2	3.7 ± 0.1	303	0.285
Sturgeon Point	9.4 ± 0.2*	176	8.4 ± 0.2	109	<0.001	9.5 ± 0.4	45	8.7 ± 0.1	196	0.057
Olson	10.5 ± 0.2	3227	11.1 ± 0.1*	9832	0.004	11.2 ± 0.3	116	11.7 ± 0.1	476	0.090
Lake Ontario										
Sunset Bay	6.2 ± 0.1	1594	5.8 ± 0.9	25	0.485	7.0 ± 0.2**	249	4.1 ± 0.1	227	<0.001
Newfane	8.7 ± 0.2*	313	7.2 ± 0.3	6	0.003	–	–	–	–	

* Significant ($p < 0.05$, t-test) size difference between boats.
** Significant ($p < 0.05$, t-test) size difference between temporary substrates.

Bossenbroek, 2008), which may lengthen the time for colonization of these environments by quagga mussels. Further, dreissenids in wetlands experience increased predation from crayfish, turtles, muskrats, and fish (Bodamer and Bossenbroek, 2008; Bulté and Blouin-Demers, 2008; Love and Savino, 1993; Perry et al., 1997; Petrie and Knapton, 1999). Zebra mussels are more resistant to such predation due to their thicker shells and tighter attachment to substrates (Casper and Johnson, 2010; Peyer et al., 2009, 2010). Therefore, such habitats may act as long-term refugia for zebra mussels.

Another source of zebra mussel veligers could be the inflowing rivers themselves, which are often dominated by zebra mussels. In general, zebra mussels are better adapted to flowing waters and shallow areas of the lakes with unstable conditions, including higher water velocities and waves (Karatayev et al., 2011).

Zebra and quagga mussels co-occur and are co-dominant in their native range in the Dnieper River Delta and the Dnieper–Bug Liman (Zhulidov et al., 2010), a shallow eutrophic coastal lake with a constant input of nutrients with the flow of incurrent rivers. This stands in contrast to lakes, where quagga mussels are likely to attain larger total population sizes and eventually outcompete zebra mussels when food is limited by having a greater energetic efficiency than zebra mussels (Mills et al., 1999; Stoeckmann, 2003). Both newly recruited and multi-year zebra mussel populations were found in six of the seven tributaries examined, and in three of these, *D. polymorpha* was dominant. We found that the proportion of zebra mussels on infested boats from marinas with tributaries was significantly greater than on boats from marinas without tributaries. In our study all marinas located on tributaries were in Lake Ontario; however, as all tributaries that we sampled in both lakes contained permanent *D. polymorpha* populations, these findings are likely to be general. Thus, even modest populations of *D. polymorpha* in the tributaries of lakes appear capable of supporting a greater presence of zebra mussels on boats and floating substrates, in spite of the overall dominance of *D. r. bugensis* in the Lower Great Lakes.

In marinas not situated on tributaries containing zebra mussels, an alternate source of *D. polymorpha* larvae is the littoral zone. In samples from both lakes, we found zebra mussels in littoral areas with extensive wave motion, and in some cases, *D. polymorpha* was locally dominant. Patchy distributions of zebra mussels have been reported previously in waterbodies dominated by quagga mussels (e.g., Zhulidov et al., 2010). This is particularly important for Lake Erie, where zebra mussels are still common in the western basin (reviewed in Karatayev et al., in review). Zebra mussel larvae may disperse with water currents driven by the prevailing northeasterly winds from the western basin throughout Lake Erie (Martel, 1993). Griffiths et al. (1991) suggested this same mechanism as the primary factor promoting the initial colonization and northeasterly expansion of *D. polymorpha* from the western basin of the lake. Therefore, the western basin of Lake Erie may presently be acting as a source of zebra mussel larvae across the whole lake.

Implications for the spread of Dreissena

D. polymorpha is more likely to resist dislodgment than *D. r. bugensis* due to its flattened ventral shell surface and higher rate of byssal thread production (Claxton et al., 1998; Dermott and Munawar, 1993; Mackie, 1991; Peyer et al., 2009, 2010). These traits make it more likely that zebra mussels will remain attached to substrates that experience stronger water currents than quagga mussels. Therefore, *D. polymorpha* may be more abundant on floating substrates, such as buoys (Conn and Conn, 2007; Diggins et al., 2004; Environment Canada, 2010) and boats, which experience greater water motion. Although zebra mussels have not been found during regular sampling of the Buffalo area of Lake Erie over the past five years, their relative abundance on navigation buoys in the same area is similar to that of *D. r. bugensis* (Karatayev et al., 2010).

For dreissenids transported to new waterbodies by boats, the likelihood of a successful invasion will depend on environmental conditions of the recipient waterbody, the number of mussels introduced, and their state of maturity. Dreissenids become sexually mature at 6–8 mm length, and fecundity increases exponentially with size (Claxton and Mackie, 1998; Lvova and Makarova, 1994). For the heavily infested boats from our study, >78% of dreissenids were of reproductive size by the end of September and capable of spawning that same season. The greater number of zebra mussels on boats and their larger size would give them a population and reproductive advantage when transported to new lakes.

Table 5
Number of dreissenids (average ± standard error) attached to boats infested with *Dreissena* found in marinas in the Lower Great Lakes.

Marina	Both dreissenids		*D. polymorpha*		*D. r. bugensis*	
	Average	Range	Average	Range	Average	Range
Lake Erie						
Buffalo Yacht Club	66.6 ± 33.3	4–156	6.3 ± 3.8	0–15	60.3 ± 32.6	4–146
Sturgeon Point	57.0 ± 8.6	28–104	35.2 ± 6.3	14–78	21.8 ± 3.6	4–42
Olson	618.3 ± 267.6	12–3940	153.9 ± 68.1	0–1140	464.5 ± 205.8	12–2820
Lake Ontario						
Sunset Bay	101.2 ± 10.1	34–205	99.6 ± 10.0	34–200	1.6 ± 0.6	0–9
Newfane	39.8 ± 13.4	9–114	39.1 ± 13.1	9–113	0.7 ± 0.4	0–3

Johnson and Carlton (1996) examined recreational boats as a vector of spread for *D. polymorpha* from marinas on Lake St. Clair. They found zebra mussels primarily on macrophytes entangled on boat trailers, rather than attached to hulls (Johnson and Carlton, 1996; Johnson et al., 2001). However, because resident boats spend extended periods in dreissenid-infested waters, attached *Dreissena* can grow to reproductive size. These dreissenids may be more likely to survive long-distance movement than veligers in small volumes of water or juveniles and adults on macrophytes entangled to boats and trailers. Prior to the invasion of Lake Mead (California), at least nineteen boats crossing into California had zebra mussels attached to their hulls or motor compartment (Benson et al., 2012). Similarly, prior to the colonization of Lake Texoma, Texas, by *D. polymorpha*, there were five documented cases of zebra mussels found on boats that were transported from other states to this lake (Texas Parks and Wildlife Department, 2009).

While the movement of resident boats to other waterbodies is far less frequent than for most trailered boats, they can carry a large number of mussels in spawning condition. Studies have suggested that these boats are the most likely vectors for the long-distance spread of mussels (Bossenbroek et al., 2007; Johnson et al., 2001, 2006), especially when they are moved to waterbodies in warmer states and are used during the winter months instead of being winterized at local marinas (Griffiths et al., 1991), or are sold to new owners across the country. Quantifying the threat of resident boats as a vector of spread, however, is problematic not only due to a lack of sufficient data regarding the number of these boats that are transported to new waterbodies, but also because the number of introduced dreissenids needed for a successful colonization is not known (Johnson et al., 2001; Padilla, 2005). Nevertheless, the large quantity of resident boats in the Great Lakes (Great Lakes Recreational Boating, 2008), molecular data suggesting Great Lakes *Dreissena* populations as the sources of dreissenid invasions in California (Brown and Stepien, 2010), and economic factors which make resident boats more likely candidates for long distance transport (Bossenbroek et al., 2007; Johnson et al., 2001, 2006), all indicate that long term resident boats in the Great Lakes may be likely sources of future zebra mussel invasions. Quantitative data on the fouling of resident boats in invaded waterbodies and the probability of their long-distance movement are essential to identifying and preventing future *Dreissena* invasions. Models and predictions of the spread of invaders based solely on numerical abundance of populations are likely to be unreliable if they do not take into account habitat-specific and vector-specific abundances of invaders.

Conclusion

Although quagga mussels compose ~99% of dreissenids in eastern Lake Erie and in Lake Ontario, on boats, zebra mussels were usually more abundant and were significantly larger than the quagga mussels at most marinas. Zebra mussel refugia were found in bays, tributaries, and in the upper littoral zones with high wave activity, areas which are usually overlooked during traditional benthic surveys. These data suggest that the relative proportion of species in an environment is not a reliable predictor of the most likely species to invade from the system. In spite of quagga mussel dominance of these ecosystems, the Lower Great Lakes still have the potential to be a source for the spread of zebra mussels. Therefore, we suggest that lakewide dominance does not predict the spread potential of dreissenids.

Acknowledgments

The authors would like to thank the marina workers of the Buffalo Yacht Club, Sturgeon Point Marina, Sunset Bay Marina, Newfane Marina, and Olson Marina. Collection of littoral samples was in part funded by U.S. EPA grants (Awards #GL00E00503 and #GL00E75301) in Lake Erie and by a U.S. Fish and Wildlife Service grant (the Great Lakes Fish and Wildlife Restoration Act award #F10AP00121) in Lake Ontario. We thank Mary F. Perrelli (Buffalo State College, Geography and Planning Department) for providing the map of sampling sites. We would also like to thank two anonymous reviewers and the editors, who provided valuable comments that improved this manuscript.

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