Biol Invasions (2012) 14:1157–1175
DOI 10.1007/s10530-011-0146-0

ORIGINAL PAPER

Low dissolved ions may limit secondary invasion of inland waters by exotic round gobies and dreissenid mussels in North America

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Received: 10 June 2011 / Accepted: 22 November 2011 / Published online: 8 December 2011

Abstract Round gobies and dreissenid mussels, exotic species in the North American Great Lakes basin, are euryhaline organisms whose geographic spread and ecological impacts in freshwaters may be limited by low levels of dissolved ions such as calcium (Ca). We measured source populations of these exotics in the St. Lawrence River and found population densities of dreissenids (range of $\sim$1,000–6,400 individuals m^{-2}) and round gobies (6–32 individuals m^{-2}) similar to those in other Great Lake locations from which they have spread inland. However, we found little evidence for their secondary invasion of inland tributary rivers and lakes of northern New York State. Using natural waters collected from inland ecosystems, we ran laboratory bioassays of reproduction, growth, and survival of several life stages of zebra and quagga mussels as well as the round goby. We found little difference in the responses of zebra and quagga mussels, with each species showing moderate reproductive success, growth, and survival at Ca concentrations > 13 mg L^{-1} and dramatic improvements at >18 mg L^{-1}. Round gobies showed moderate survival in waters with Ca concentrations > 8 mg L^{-1} and high survival > 18 mg L^{-1}. These bioassays are the first such experiments for quagga mussels and round gobies and show how all three species may be similarly restricted in their ability to invade and permanently colonize significant geographic regions of New York State and perhaps the US.

Keywords Secondary invasion · Round goby · Zebra mussel · Quagga mussel · Specific conductivity · Inland waters

Introduction

Several aquatic exotic species in North America initially colonized and impacted the Laurentian Great Lakes (Jude et al. 1992; Mills et al. 1993; Ricciardi and MacIsaac 2000) and secondarily invaded connected waterways or smaller inland lakes in their watersheds. Secondary invasions by zebra mussels (*Dreissena polymorpha*) have been studied extensively (Koutnik and Padilla 1994; Mellina and Rasmussen 1994; Miller and Haynes 1997; Schneider et al. 1998; Kraft and Johnson 2000; Allen and Ramcharan 2001; Drake and Bossenbroek 2004; Frischer et al. 2005; Bossenbroek et al. 2007; Whittier et al. 2008; Drake and Bossenbroek 2009) and recent attention has focused on the inland spread of the round

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goby (*Neogobius melanstomus*) (Phillips et al. 2003; Irons et al. 2006; Krakowiak and Pennuto 2008; Kornis and Vander Zanden 2010; Poos et al. 2010). Although we have reasonable certainty in models developed to predict further spread of zebra mussels in North America, such information is far more limited for quagga mussels (*Dreissena rostriformis bugensis*) and round gobies, especially for ecosystems with low levels of dissolved ions.

Predictions of secondary invasions consider a variety of factors such as the environmental tolerances and natural history traits of the organism as well as human transfer mechanisms. Because they are euryhaline, substantial work has examined maximum salt tolerance of dreissenids and round gobies inhabiting inland seas and estuaries, as well as their ability to tolerate ship ballast water (Ludyanskiy et al. 1993; Kilgour et al. 1994; Mills et al. 1996; Moskal'kova 1996; Charlebois et al. 1997; Setzler-Hamilton et al. 1997; Wright et al. 1996; Karatayev et al. 1998; Reid and Orlova 2002; Corkum et al. 2004; Ojaveer 2006; Ellis and MacIsaac 2009). Within freshwaters, however, it is the lack of dissolved ions that may limit the spread and impact of these exotics. Considerable attention has been given to this very issue for the zebra mussel and the general consensus is that they are unable to colonize waters with low levels of dissolved ions (commonly measured as specific conductivity, or SC), particularly low concentrations (<8–12 mg L^{-1}) of calcium (Ca) needed for shell growth and physiological functions (Sprung 1987; Neary and Leach 1992; Ramcharan et al. 1992; Vinogradov et al. 1993; Mellina and Rasmussen 1994; McMahon 1996; Hincks and Mackie 1997; Frischer et al. 2005; Jones and Ricciardi 2005; Whittier et al. 2008). By comparison, far less is known about this tolerance for quagga mussels and yet in geographic distribution models they are assumed to act similar to zebra mussels (Whittier et al. 2008). Although they do share great biological overlap with zebra mussels, quagga mussels have notable differences in bioenergetics, growth, shell mass, and colonization patterns (Mills et al. 1996; Claxton et al. 1998; Mills et al. 1999; Baldwin et al. 2002, Stoeckmann 2003; Casper and Johnson 2010; USGS 2011a). Could their tolerance to SC and Ca differ from zebra mussels as well? To date we only know that quagga mussel populations in the St. Lawrence River (SLR) seem restricted to Ca concentrations higher than 12 mg L^{-1} (Jones and Ricciardi 2005) and that they appear to tolerate higher Ca levels than zebra mussels (Zhulidov et al. 2004; Jones and Ricciardi 2005). Further examination of their tolerance, across their life history, would be helpful to confirm or refine distribution models.

Likewise, we know that the round goby, a co-evolved predator of zebra and quagga mussels, has colonized and impacted the Great Lakes and certain of their tributary rivers but only waters with moderate SC. Is their spread also limited by low SC and will such waters remain ecological refuges to their spread and impact? Round gobies are widely established (USGS 2011b) in Lakes Huron (SC ~ 210; USEPA 2011), Michigan (SC ~ 290), Erie (SC ~ 282), and Ontario (SC ~ 300) as well as the International Section of the SLR (SC ~ 300; Hickey and Fowlie 2005; Farrell et al. 2010, M. Carpenter and B. S. Baldwin pers. obs.). By comparison, their very limited distribution in Lake Superior may, in part, be due to the lower levels of dissolved ions in the lake (SC ~ 100). The secondary invasion of round gobies in North America is underway and they have colonized and impacted tributaries of Lakes Erie (Krakowiak and Pennuto 2008; Poos et al. 2010), Huron (Poos et al. 2010), Michigan (Kornis and Vander Zanden 2010) as well as the Mississippi river basin (Irons et al. 2006), all of which have moderate SC levels (~260–900; Krakowiak and Pennuto 2008; K.S. Irons, Illinois Department of Natural Resources, pers. comm.; M.S. Kornis, University of Wisconsin, pers. comm.). In contrast, we have noticed (B. S. Baldwin, pers. obs.) negligible spread from the SLR into major tributaries of northern New York (Fig. 1), all of which have SC ~ 160 and lower (Chiarenzelli et al. 2011; B. S. Baldwin unpublished data).

The goals of this study were to (a) assess secondary invasion of dreissenids and round gobies in northern New York (NNY) rivers and lakes and (b) use laboratory bioassays to compare the tolerance of quagga mussels and round gobies to low SC with that of the zebra mussel. The NNY region is an appropriate place to study a potential restriction to secondary invasion because the SLR has reproducing source populations of mussels and gobies which could spread into (naturally and with human facilitation) tributary rivers and inland lakes that drain a watershed whose geology becomes more resistant to dissolution with distance from the SLR (Chiarenzelli et al. 2011).

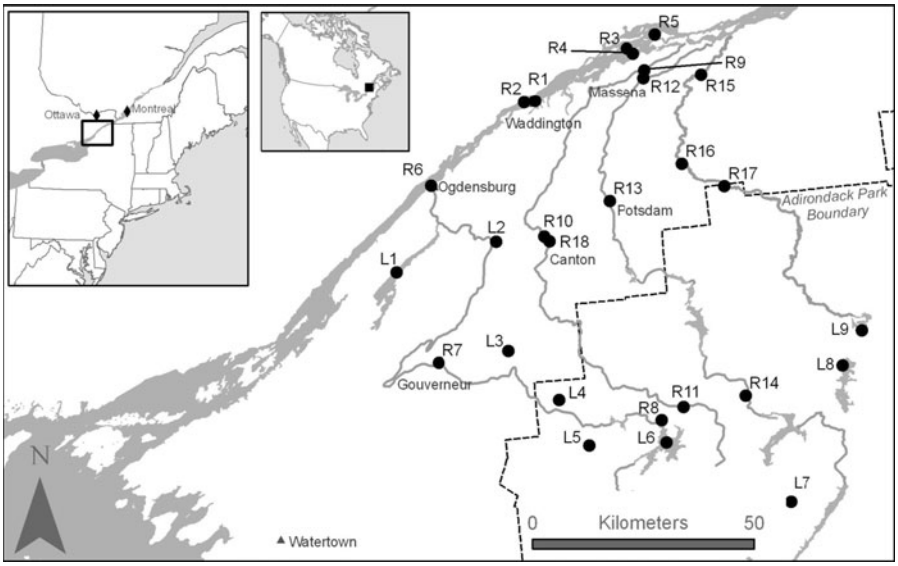

Fig. 1 Sampling locations in the St. Lawrence River, in four tributary rivers draining northern New York, and inland lakes of this watershed. Site codes are explained in Table 1

Because of these characteristics we felt our work could provide useful data for modeling efforts that consider similar geologic regions in North America. Given the euryhaline adaptations they evolved in their native Ponto-Caspian region (Reid and Orlova 2002) we predicted that quagga mussels and round gobies would generally have similar tolerances to zebra mussels, the exception being that quagga mussels would be better suited to higher SC and Ca levels. Collectively, we anticipate that our NNY region, and others like it, will be lightly colonized and largely immune to the impacts of these nuisance species.

Methods

Field surveys

Dreissenid and round goby populations in the SLR were measured during midday, from June to September 2008, to determine source population levels that might support secondary invasions into NNY tributaries and lakes. We focused on Lake St. Lawrence, a fluvial lake between the Iroquois Dam ($\sim$126 km downstream from its outlet at Lake Ontario) and the Moses-Saunders Power Dam ($\sim$171 km). Confluences of four major NNY tributaries are near this area (Fig. 1) and, with the Lake as a major recreational boating and fishing area, inadvertent human transfer may exist between the lake and a host of inland waters. We also hoped that our data would fill an important regional gap between similar surveys in the uppermost SLR (Farrell et al. 2010) and downstream surveys of dreissenids near Montreal (Jones and Ricciardi 2005).

Dreissenid populations were SCUBA surveyed in profundal zone sites (some nearshore, some farther offshore) near the villages of Waddington and Massena (Fig. 1). All sites were beyond the ice-impacted littoral zone. Sampling depths ranged from 6 to 30 m and the riverbed substrate was a mixture of mud, sand, large rocks, and exposed bedrock. At each site, 6–8 quadrats (0.0625 m^2) were placed on the riverbed at about 5 m intervals along a 50 m transect oriented perpendicular to the shore. All zebra and quagga mussels within a quadrat were gathered and placed in plastic bags for laboratory analyses. Live mussels were counted (population densities reported as individuals m^{-2}) after sorting to species and shell length categories ($<$0.5, 0.5–1, $>$1–2, $>$2 cm). The two small size categories indicate young of the year (YOY) mussels while the larger sizes were mainly adults.

Round goby populations in these same sites were measured using SCUBA and underwater video capture. Prior to dreissenid sampling (to minimize disturbance), a high-definition video camera (Sony HDR-HC9 HDV Camcorder inside a Backscatter Top Dawg Video Housing) was positioned atop a 1 m tall tripod to film a 1–2 m^2 area of riverbed 1–3 m in front of the tripod. Divers moved several meters away during recording. After 10 min of filming, a 0.25 m^2 quadrat, marked with 1 cm scale bars, was placed in the same field of view and filmed (for an additional

2–3 min) as a scaling reference to be used later in video analysis. The borders of the quadrat, its scale bars, the enclosed riverbed features, and fish (about $\geq$3 cm total length) could be seen in high resolution. We were less confident seeing fish < 3 cm and so counts rarely included those individuals (thus our estimates exclude many juveniles and may underestimate total goby populations). Filming was repeated at 5–6 haphazardly chosen sites near our dreissenid collection areas.

Earlier attempts to film gobies while moving along a bottom transect (see Johnson et al. 2005; Lederer et al. 2006; Taraborelli et al. 2009) were problematic in that the process normally scared fish away from the filmed area and did not produce images where we were able to see gobies clearly enough for quantification. During placement of our mounted camera, some gobies directly under the tripod (area not filmed) were disturbed and moved away. However, within 2–5 min, gobies resumed their typical, seemingly haphazard movement patterns along the riverbed, showing no interest in or avoidance of the tripod and camera. Preliminary video analyses of 30 min long film clips, started as soon as a diver set the tripod and turned on the camera, showed that goby counts taken at 1 min intervals did not change significantly with time (ANOVA, $P < 0.01$), suggesting that gobies in the filmed areas were neither attracted nor repelled by our tripod and camera. As a precaution, however, in our subsequent protocol of using 10 min film clips, we considered the first 5 min of film as an acclimation period for gobies, and only the final 5 min of film was used for population estimates.

In the laboratory, filmed gobies were enumerated on a computer monitor that had been marked with the outline of the scaling quadrat for that site and film clip. Once the quadrat was outlined (by viewing film in the 10–13 min interval), the film was rewound to the beginning of the clip and played at normal speed. After the 0–5 min acclimation period, and during the 5–10 min interval, the film was slowed and paused around distinct 1 min intervals to allow counting of gobies seen within the scaling quadrat (i.e. gobies in the 0.25 m^2 area). Interval counts were averaged to derive population density estimates (individuals m^{-2}) for each replicate film location at each river sampling site. Total body length (TL) of round gobies, whose bodies were aligned with and adjacent to the horizontal portions of the marked scaling outline, were estimated using the 1 cm scale bars on the outlined quadrat. Other gobies seen within the quadrat were counted but not used for size estimates. We used TL (cm) categories of 3–6, 6–9, and 9–12 as general estimates of population size structure.

We also surveyed SLR tributary rivers and inland lakes for dreissenid mussels and round gobies (Fig. 1) as part of a separate long term survey (1996–2010) of native invertebrates and fish in NNY (B.S. Baldwin, unpublished data). In rivers, we typically sampled biota along 50 m stretches, conducting kick samples (Bode et al. 2002) in 10–12 locations using D-nets 45 cm wide with 1 mm mesh. Macroinvertebrates were preserved in 70% ethyl alcohol and identified in the laboratory. For the purposes of this study, we only report presence/absence of dreissenids. We also used a bag seine ($\sim$9 m long with 3 mm mesh) and baited minnow traps (left 2–6 h) to sample fish communities at these sites. Fish were identified in the field to family and then released. Here too, we only report presence/absence of round gobies. In lakes, we conducted qualitative visual surveys of the benthos by snorkeling in the littoral zone or scuba diving in the profundal zone. In cases where dreissenids were found, they were collected, identified, and sized.

At field locations we also measured water temperature, pH, dissolved oxygen (DO), SC, and suspended chlorophyll a (Chl a) using a Hydrolab Datasonde 4a. For field sites in the SLR, these measurements were made on the riverbed in 2008 but for NNY tributary river and lake locations measurements were conducted for most if not all years in the long-term study. At most sites a 0.5 L sample was collected in a clean plastic bottle and returned to the laboratory for analysis of total water hardness (LaMotte kit, PHT-DR-LT). Concentrations of dissolved calcium were measured in similar samples by the Adirondack Aquatic Institute at Paul Smith's College, NY and the Adirondack Lakes Survey Corporation in Ray Brook, NY, each using USEPA protocols (USEPA 1987, 1991).

Laboratory experiments

While we assessed secondary invasions of our NNY tributaries and lakes with field surveys (above) we also used quarantined laboratory experiments to judge the potential of these exotics to tolerate the chemical conditions present in these natural waters, should they invade. Here, we compared their growth and/or survival in SLR water (control), deionized (DI) water (negative control) and natural waters collected from a variety of regional rivers and lakes (Table 1; Fig. 1). Studies were conducted between 2005 and 2009. As a reference organism, we ran tests on all life stages of the better studied zebra mussel and compared results to the lesser studied quagga mussel and round goby. All animals were collected from our nearshore SLR site near Waddington.

Our first test, judging the scenario of whether transported juvenile and adult dreissenids could grow and survive in inland NNY waters, was conducted following a 2-week acclimation of collected animals to laboratory holding conditions in SLR water from Waddington. For experiments, each species was tested separately, as were adults (14–16 mm shell length), and juveniles (4–6 mm). Thirty animals were tested in each of the 11 experimental conditions, with each mussel reared individually at 20°C in separate aerated beakers holding 0.5 L of their test water (modified from Baldwin et al. 2002). We tested growth and survival in natural waters from 3 rivers, 5 lakes, 2 dilutions of SLR water, and the DI control, all of which spanned Ca concentrations of about 0–32 mg L^{-1} (Table 1). Natural waters were collected within a week of use in experiments. To focus dreissenid responses on water chemistry, we removed the vast majority of natural planktonic foods by prefiltering test waters (Gelman A/E filter; nominal pore size ~ 1 µm) and provided all animals with uniform levels of live, cultured algae (*Chlamydomonas* sp.) that were added to each beaker during daily water changes (target concentration 5×10^8 cells L^{-1}). Animals were reared under a light:dark cycle of 14:10 h.

Survival was assessed every 2 days (dead mussels gaped and did not respond to touch) and growth was measured by comparing body mass at the beginning and end of the experiments, which ran 65 (adult) and 58 (juvenile) days. We measured change in wet mass (WM; live soft tissue + shell mass) as the most accurate assessment of total mussel growth (3-dimensional changes in shell and tissue). Individual live animals were dried externally with a tissue and weighed on an OHAUS Voyager Pro balance to the nearest 0.1 mg. We report mussel growth as percentage change in WM ($100 \times$ (final mass $-$ initial mass)/initial mass).

The second scenario we tested was whether transported adult dreissenids might spawn within inland waters and here we made comparisons of gamete fertilization in each test water (modified from Baldwin et al. 1996). Adult mussels were collected from the SLR at Waddington in May when water temperatures were 8–12°C. In the laboratory, mussels were brushed clean, allowed to clear their digestive tracts in filtered (1 µm) SLR water, moved to clean containers and water, and then spawned at 18°C. Mussels were spawned in separate glass jars within 2 h of stimulation with 1 mmol L^{-1} serotonin. Eggs from 5 parents were mixed and about 1,000 eggs were pipetted into 3 separate 200 ml jars for each different test water (Table 1). Sperm from 5 parents were also mixed but left in jars containing SLR water. After a 30 min acclimation period for eggs in each test water, sperm was added (sperm:egg ratio apprx. 5–10) to test fertilization success in each test water jar. Fertilization was checked microscopically (200 eggs viewed per jar) and assessed as the proportion of observed eggs that were dividing (i.e. were zygotes) at 2 h post-insemination.

In a third scenario, we tested whether SLR mussel zygotes or veligers might survive direct innoculation into inland waters. Here, additional mussels were spawned and eggs were fertilized in SLR water in the laboratory. At 2 h post-insemination, 50 zygotes were pipetted into 3 separate petri dishes for each of the test waters used above and raised for an additional 48 h to assess the proportion of zygotes that survived and developed to the D-veliger stage (for review of dreissenid larval stages, see Ackerman et al. 1994). To test veliger survival, additional mussels were spawned in the laboratory and eggs were fertilized and reared for about 1 week in SLR water (to the umbo veliger stage; about 120 µm shell length). Subsets of these larvae ($n = 50$) were transferred into the same test waters used above. Larvae were reared individually in 5 ml chambers of tissue culture plates and were monitored microscopically for another 10–14 days for survivorship to the pediveliger stage. In all treatments, waters were filtered (1 mm), changed every 2 days, and larvae were fed cultured *Nannochloris* sp. daily at a target concentration of 5×10^8 cells L^{-1} (modified from Baldwin and Newell 1995).

Laboratory tests for round gobies examined a scenario where gobies from the SLR might spread upstream into tributaries (or be transported by humans) and thus we used test waters from the SLR and sections of our tributary rivers. We included a 50% SLR treatment to represent SC/Ca levels

Table 1 Sample sites and environmental conditions (means ± SD) of the St. Lawrence River (SLR) and its tributary rivers (site codes, R) as well as lakes (L) in NNY, 1996–2010

Site code	Site name	Lab test	Calcium concentration (mg L^{-1})	Total hardness (mg $CaCO_3$ L^{-1})	Specific conductivity (μS cm^{-1})	pH
R1	SLR Waddington nearshore	ZQ, RG	32.07 ± 1.28	130 ± 5.72	299 ± 4.49	8.45 ± 0.59
R2	SLR Waddington offshore		28.12 ± 1.12	130 ± 4.16	299 ± 3.89	8.55 ± 0.34
R3	SLR Massena nearshore		26.47 ± 0.98	126 ± 6.80	296 ± 5.33	8.74 ± 0.70
R4	SLR Massena offshore Long Sault		27.98 ± 0.87	130 ± 5.20	298 ± 5.66	8.71 ± 0.35
R5	SLR Massena offshore Barnhart		27.18 ± 1.03	126 ± 6.05	295 ± 3.25	8.81 ± 0.26
R6	Oswegatchie R. downstream	RG	8.14 ± 0.28	44 ± 1.06	108.7 ± 24.76	7.57 ± 0.92
R7	Oswegatchie R. midstream	RG	5.03 ± 0.17	30 ± 1.92	78.2 ± 19.54	7.45 ± 0.84
R8	Oswegatchie R. upstream		1.14 ± 0.04	8 ± 0.31	25.5 ± 2.45	7.22 ± 0.54
R9	Grasse R. downstream	RG	8.19 ± 0.27	44 ± 1.33	109.1 ± 26.64	7.57 ± 0.92
R10	Grasse R. midstream	RG	5.22 ± 0.23	32 ± 1.39	80.1 ± 18.84	7.46 ± 0.84
R11	Grasse R. upstream		2.74 ± 0.10	22 ± 1.10	55.8 ± 7.29	7.36 ± 0.55
R12	Raquette R. downstream	RG	2.50 ± 0.09	22 ± 0.75	53.5 ± 13.02	7.35 ± 0.82
R13	Raquette R. midstream	RG	2.29 ± 0.09	20 ± 0.80	51.4 ± 12.53	7.34 ± 0.78
R14	Raquette R. upstream	RG	0.71 ± 0.01	12 ± 0.66	36 ± 4.98	7.28 ± 0.54
R15	St. Regis R. downstream	RG	5.24 ± 0.14	32 ± 1.52	80.3 ± 19.35	7.46 ± 0.91
R16	St. Regis R. midstream	RG	1.30 ± 0.03	14 ± 0.53	41.7 ± 12.42	7.30 ± 0.87
R17	St. Regis R. upstream		0.47 ± 0.02	8 ± 0.35	33.6 ± 3.72	7.76 ± 0.62
R18	Little River	ZQ	23.64 ± 0.87	104 ± 6.66	217.1 ± 3.04	8.18 ± 0.57
L1	Black Lake	ZQ	17.96 ± 0.64	72 ± 2.74	161.8 ± 2.43	8.08 ± 0.48
L2	Lower Lake	ZQ	13.50 ± 0.55	68 ± 3.94	127.5 ± 2.04	7.64 ± 0.31
L3	Trout Lake		4.70 ± 0.14	68 ± 3.67	75 ± 0.90	8.73 ± 0.57
L4	Partlow Pond	ZQ	6.16 ± 0.20	24 ± 1.20	54.7 ± 0.71	7.37 ± 0.55
L5	Twin Lakes	ZQ	7.89 ± 0.33	36 ± 1.08	152.8 ± 2.75	7.39 ± 0.58
L6	Cranberry Lake	ZQ	2.03 ± 0.05	8 ± 0.38	23.6 ± 0.42	7.05 ± 0.37
L7	Mohegan Lake		2.11 ± 0.04	6 ± 0.24	33.1 ± 0.63	7.12 ± 0.21
L8	Upper Saranac Lake	ZQ	4.19 ± 0.14	22 ± 0.97	58.4 ± 0.76	7.25 ± 0.33
L9	St Regis Lake		3.73 ± 0.16	18 ± 0.43	49.8 ± 0.75	7.16 ± 0.40
	Range		0.47–32.07	6–130	23.6–229.0	7.05–8.81
	DI water	ZQ, RG	0.07 ± 0.01	0 ± 0.00	2.2 ± 0.04	5.89 ± 0.25
	30% SLR Waddington nearshore	ZQ	9.38 ± 0.32	42 ± 3.42	96.3 ± 13.14	8.23 ± 0.47
	40% SLR Waddington nearshore	ZQ	12.26 ± 0.37	54 ± 4.63	121.8 ± 14.62	8.31 ± 0.51
	50% SLR Waddington nearshore	RG	18.24 ± 0.46	72 ± 6.63	161.5 ± 16.02	8.36 ± 0.43

Certain natural or amended waters were also used for zebra mussel (Z), quagga mussel (Q), or round goby (RG) lab tests, 2005–2009. Deionized water (DI) was used in some tests as a negative control or was added to SLR water to dilute it to 50, 40, and 30% of ambient concentrations

measured in lower tributaries during drier years. We examined the survival of large SLR gobies (6–9 cm TL; assumed to be late stage juveniles or adults according to MacInnis and Corkum 2000; French and Black 2009) and small newly settled young of the year (YOY, 1–2 cm TL) gobies held in test waters collected from up- and downstream sections of four SLR tributary rivers, which themselves spanned a range of SC and Ca concentrations (Table 1). Some test waters, despite coming from different sites, had similar SC/Ca values but were still tested to ensure geographic representation. In total, 12 experimental conditions were tested for both large and small fish. For each test water, large fish (in groups of 3 individuals) were reared in 10 replicate aquaria (5 gallon each). YOY were also reared in 10 aquaria (1 gallon) but each contained groups of 5 individuals. All aquaria contained aerated control or test waters, gravel, and sections of PVC pipe (one for each fish) as benthic habitat. Aquaria were kept at 20°C and were exposed to a light:dark cycle of 14:10 h. All fish were initially held in SLR water for a week to acclimate to laboratory conditions. Aquarium water was then changed gradually over a 24 h period to our test conditions and survival was observed for up to 63 days (large gobies) and 67 days (small gobies). Dead fish were noted and removed from the aquarium. Moribund fish (scored as mortalities) were euthanized using tricaine methanesulfonate (MS-222, in accordance with University animal care criteria).Test waters were changed twice a week and fish were fed blackworms or shrimp pellets once each day, in excess. The ventilation frequency of our large fish was measured for each individual as a potential indicator of physiological stress (Barreto and Volpato 2004). Rates were measured once, within the first week of the experiments in test waters, on a day prior to a water change. Following a 10 min acclimation of the fish to the human viewer positioned near the aquarium, the opercular beats of individual fish were viewed and counted during a known interval between 5 and 10 min.

Statistical analyses

Survival and fertilization data were analyzed using binary logistic regression since we were considering a dependent variable that is inherently binary (animals survived or died, eggs were fertilized or not). Traditional linear regression was not appropriate here since for binary data the variance is a function of the expected value (Sinnich and Mendenhall 2003). Data on dreissenid growth and round goby ventilation did not pass normality and equal variance tests and thus the main effects of Ca concentration, animal species, and/or size/age were analyzed using the non-parametric Kruskal–Wallis ANOVA on ranks. We took a stepwise model building approach that began with full models testing main effects, along with their interactions, on biological responses. We then removed insignificant predictors from the final, reported model outcomes. We analyzed data using Minitab (statistical software, version 16) or R (statistical software, version 2.13).

Results

Natural populations

During summer 2008 benthic community structure in the SLR was visibly dominated by dreissenid mussels and round gobies. Round gobies were observed everywhere we dove, from the littoral zone to about 30 m depth, regardless of whether driessenids were present. Few other macroinvertebrates or demersal fishes were observed while scuba diving, filming, or sample processing in the laboratory. However, mussels and round gobies were rarely observed as we passed over muddy sites. For both dreissenid species, large individuals (>1 cm) were numerically dominant (Table 2), and there were negligible numbers of small YOY (<0.5 cm) settling into the benthos through

Table 2 Sample sites and population characteristics of dreissenids in the St. Lawrence River, summer 2008

Site	Dreissenid density (individuals m^{-2})	Dreissenid species	Percent of population	Percent in size classes (cm)		
				<0.5	0.5–1	>1
Waddington nearshore	1,274.6 ± 394.2	Zebra	55.8	0.0	0.1	99.9
		Quagga	44.2	0.8	5.2	94.0
Waddington offshore	1,684.7 ± 401.7	Zebra	10.4	0.0	0.0	100.0
		Quagga	89.6	0.0	9.2	90.8
Massena nearshore	5,997.3 ± 514.1	Zebra	14.4	0.0	1.0	99.0
		Quagga	85.6	0.3	3.5	96.2
Massena offshore Long Sault	1,292.7 ± 304.8	Zebra	25.8	0.0	0.0	100.0
		Quagga	74.2	0.7	2.7	96.6
Massena offshore Barnhart	2,319.9 ± 670.0	Zebra	16.4	0.0	3.8	96.2
		Quagga	83.6	0.0	2.7	97.3
All Sites	2,265.0 ± 1,678.7					

Density reported as mean ± SD (n = 6–8 analyzed quadrats per site)

September. Quagga mussels were numerically dominant at all sites except the nearshore Waddington site. Mean dreissenid density for all sites was 2,265 individuals m^{-2}, although densities from individual quadrats ranged from about 1,000–6,400 individuals m^{-2}.

The overall average density of gobies was 16.9 individuals m^{-2} (Table 3) with a range of 6–32 individuals m^{-2}. Occasionally, during general scuba surveys across the riverbed, we did observe feeding aggregations on dreissenids ("feeding frenzies") estimated as high as 200–300 individuals m^{-2}. We also observed the appearance of benthic YOY in August (estimated while diving to be as abundant as 200–400 individuals m^{-2}) but these small individuals (1–2 cm TL) could rarely be detected during video analysis. Gobies ranged in size from 3 to 12 cm TL but the majority of gobies we could measure were 3–6 cm (Table 3). Because we were less certain counting and measuring small juvenile fish (<3 cm), similar to other studies using video analysis (e.g. Schaner et al. 2009), we feel our density estimates emphasize adult populations and underestimate total round goby populations.

In our companion long term survey of NNY inland waters (1996–2010; B. S. Baldwin, unpublished data) we did not detect dreissenids or round gobies in any of our surveyed inland waters, with the exception of Black Lake (Fig. 1; site L1). Here, zebra mussels were detected in 2002 and became widespread in the littoral zone by 2010, and included adults and YOY attached to rocky substrates. No quagga mussels were detected in Black Lake. We saw no live native mussels in our SLR sites (empty shells were present and overgrown with dreissenids) but they were present in all tributaries and inland lakes surveyed from 1996 to 2010.

Table 3 Sample sites and population characteristics of round gobies in the St. Lawrence River, summer 2008

Site	Density (individuals m^{-2})	Percent in size classes (cm)		
		3–6	6–9	9–12
Waddington nearshore	9.6 ± 3.0	84.6	14.3	1.1
Waddington offshore	23.6 ± 4.3	93.6	5.2	1.2
Massena nearshore	17.6 ± 4.2	88.3	9.1	2.6
Massena offshore Long Sault	20.1 ± 6.2	93.7	5.4	0.9
Massena offshore Barnhart	14.0 ± 3.3	84.9	15.1	0
All sites	16.9 ± 6.5			

Density reported as mean ± SD (n = 5–6 analyzed quadrats per site)

Environmental conditions

During the 2008 field season in the SLR, mean water temperature on the riverbed ranged from 18.4°C in June to 21.6°C in September. We measured uniform levels of pH (mean 8.65), SC (mean 295 µS cm^{-1}), DO (mean 7.49 mg L^{-1}), and Chl a (mean 1.21 µg L^{-1}) at our sites during this summer period. In general, water near the benthos seemed well mixed, well buffered and oxygenated (always above the EPA recommended 5 mg L^{-1} minimum for fish health; Bain 1999). Levels of chlorophyll were generally oligotrophic (Cooke et al. 1993) and yet water clarity remained only modest (rarely exceeding 3 m), suggesting a high load of suspended detritus and inorganic particles.

In our companion long term survey of NNY inland waters (1996–2010; B. S. Baldwin, unpublished data) we found levels of temperature, pH (Table 1), and Chl a to be within the accepted tolerance ranges of dreissenids (McMahon 1996) and round goby (Charlebois et al. 1997). Most ecosystems also had suitable DO levels but several lakes had hypoxic (between 1 and 30% saturation) to anoxic profundal zones in summer and winter. Also, certain water bodies had low SC levels and associated Ca concentrations (Table 1). Compared to the SLR these inland waters were generally more dilute, especially areas sampled closer to the Adirondack mountains (e.g. upstream stretches of rivers). We also found SC levels to vary with year and season, becoming more dilute in heavy rainfall or spring runoff conditions.

Dreissenid tolerance experiments

In our laboratory test judging whether transported juvenile and adult dreissenids could survive and grow in test waters over about 60 days, statistical analysis (binary logistic regression) showed that survival was significantly affected by Ca concentration, mussel age group, mussel species, and the interaction of Ca concentration × species, but not the interaction of Ca concentration × age ($P = 0.173$). The results of the final model, without this latter nonsignificant interaction term (see Methods), are given in Table 4. Overall, adults survived better than juveniles and the only treatment that killed all adults was that using DI water

Table 4 Results of the binary logistic regression test of dreissenid mussel survival in test waters with different Ca concentrations

Predictor	Coef	SE Coef	Z	*P*	Odds ratio	95% Lower	CI upper
Constant	−0.149955	0.176277	−0.85	0.395			
Ca	0.176582	0.016947	10.42	0.000	1.19	1.15	1.23
Species	−1.136560	0.269925	−4.21	0.000	0.32	0.19	0.54
Age	−1.755620	0.156998	−11.18	0.000	0.17	0.13	0.24
Ca × Species	0.125511	0.029078	4.32	0.000	1.13	1.07	1.20

Main effects include Ca concentrations, mussel species, and mussel age group

(Fig. 2). The survival of mussels in both age groups was positively related to Ca up to concentrations of about 6 mg L^{-1} (adults) and 13 mg L^{-1} (juveniles), beyond which survival was high ($\geq$0.8) and nearly independent of Ca. Zebra mussels survived better than quagga mussels over low levels of Ca but at higher levels, the survival of quagga mussels was superior. The binary logistic regression equation relating the probability of mussel survival (PS) to Ca concentration (Cac) is:

$$\mathrm{PS} = \mathrm{e}^{-0.149955+0.176582\times \mathrm{Cac}-1.13656\times \mathrm{Q}-1.75562\times \mathrm{J}+0.125511\times \mathrm{Cac}\times \mathrm{Q}} / \left(1+\mathrm{e}^{-0.149955+0.176582\times \mathrm{Cac}-1.13656\times \mathrm{Q}-1.75562\times \mathrm{J}+0.125511\times \mathrm{Cac}\times \mathrm{Q}}\right)$$

where Q = 1 if quagga mussel or 0 if zebra mussel, and J = 1 if juvenile or 0 if adult.

Were surviving mussels in good enough physiological condition to grow over these Ca levels? Statistical analysis (Kruskal–Wallis ANOVA) showed that growth of mussels increased significantly with Ca concentration ($H = 770.15$, $df = 10$, $P = 0.000$), was significantly higher in juveniles than adults ($H = 109.86$, $df = 1$, $P = 0.000$), and was significantly higher in quagga mussels than zebra mussels ($H = 13.12$, $df = 1$, $P = 0.000$). Growth of all animals was positively related to Ca concentrations but we only detected net positive growth at Ca concentrations $\geq$ 9 mg L^{-1} (Fig. 3). Growth of adults appeared independent of Ca at concentrations $\geq$ 24 mg L^{-1} and independent for juveniles at Ca concentrations $\geq$ 17 mg L^{-1}.

Our tests judging potential reproductive success in transported mussels generally indicated that it could only happen in water with Ca concentrations $\geq$ 13 mg L^{-1} (Fig. 4). In the simulation of transferring reproductive SLR dreissenids into test waters, statistical analysis (binary logistic regression) showed that fertilization was significantly higher at high Ca concentrations and was higher for quagga mussels than zebra mussels (Table 5). The interaction of Ca concentration × species was not significant ($P = 0.932$). Fertilization occurred at Ca concentrations as low as

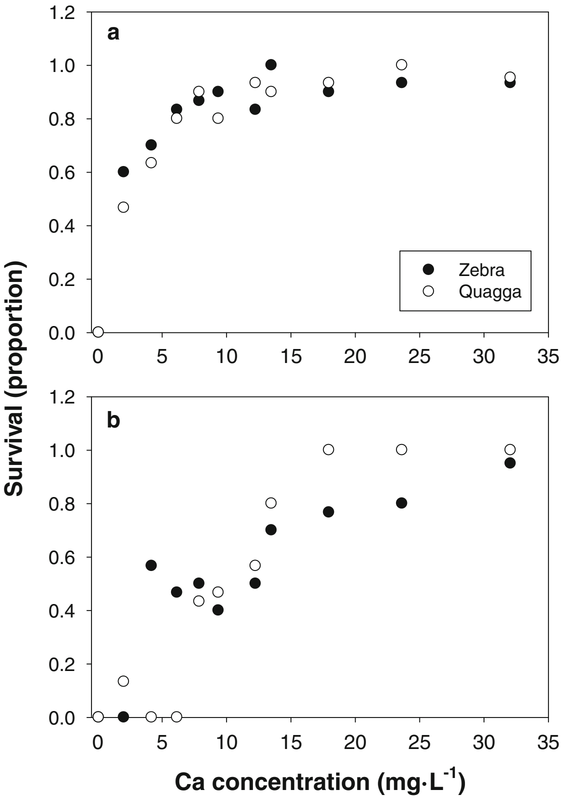

Fig. 2 Survival of adult (**a**) and juvenile (**b**) dreissenids held for 65 (adult) or 58 (juvenile) days in test waters (see Table 1) spanning a range of dissolved calcium (Ca) concentrations. Data are proportions of initial 30 individuals alive in each treatment at the end of the experiment (there are no SD error bars to report). Some data showing response values of zero for quagga mussels mask zero response symbols for zebra mussels. A binary logistic regression analysis showed that survival increased with Ca concentration ($P = 0.000$) and mussel age ($P = 0.000$), and that zebra mussel survival was superior over low Ca concentrations while quagga mussels survival was superior over high Ca concentrations ($P = 0.000$)

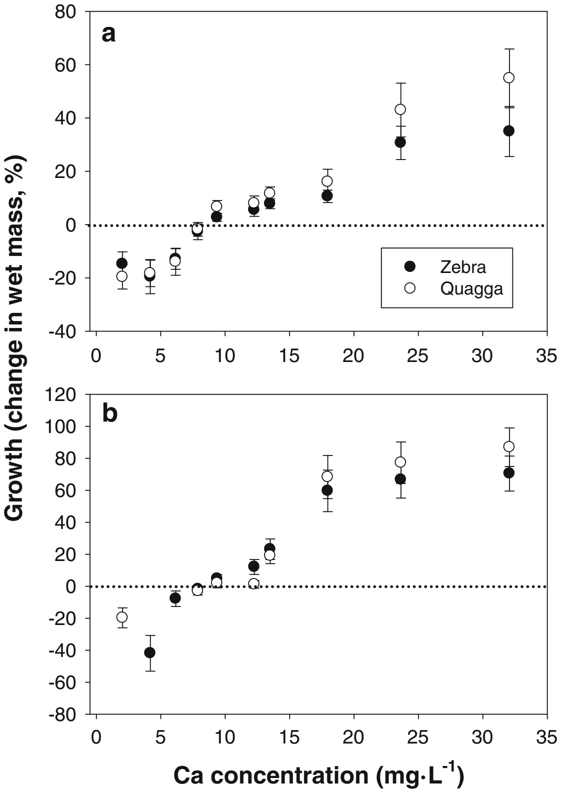

Fig. 3 Growth of adult (**a**) and juvenile (**b**) dreissenids held for 65 (adult) or 58 (juvenile) days in test waters (see Table 1) spanning a range of dissolved calcium (Ca) concentrations. Data are means ± SD, shown for those treatments with surviving animals (n = 14–30). *Dashed line* highlights level of zero growth. A Kruskal–Wallis ANOVA showed that growth increased with Ca concentration ($P = 0.000$), was higher in juveniles ($P = 0.000$), and was higher for quagga mussels ($P = 0.000$)

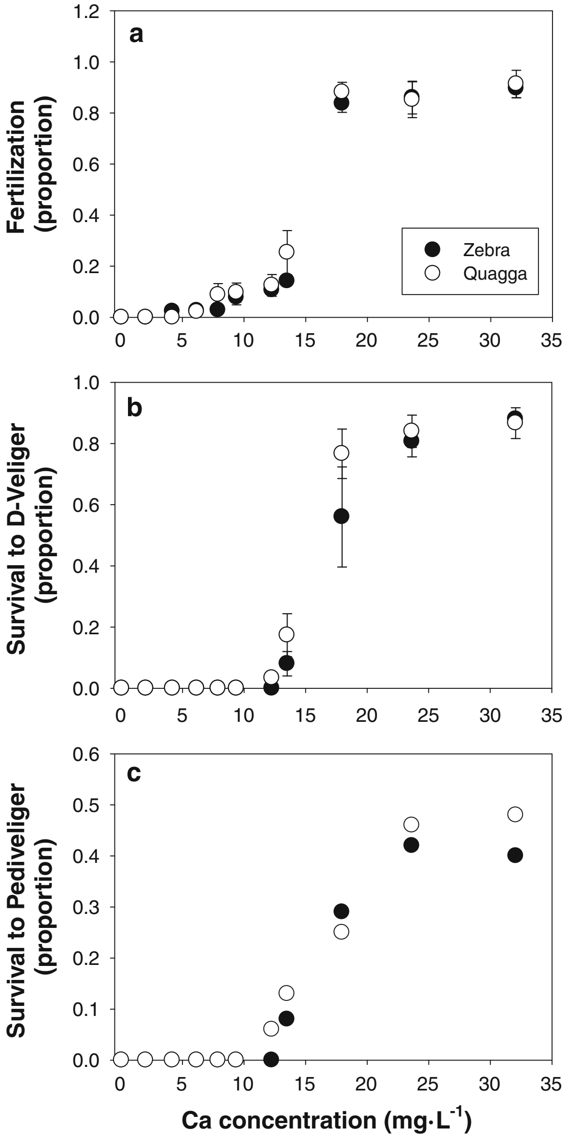

Fig. 4 Proportion of eggs fertilized (**a**), zygotes developing to D-veligers (**b**), and veligers surviving to pediveligers (**c**) for dreissenids tested in waters (see Table 1) spanning a range of dissolved calcium (Ca) concentrations. Data are mean (±SD) proportions of 3 sets of 200 inseminated eggs that fertilized in each test water (**a**), mean (±SD) proportions of 3 sets of 50 zygotes that survived to D-veliger in each test water (**b**), and the overall proportion of 50 veligers that survived to pediveliger in each test water (**c**) (there are no SD error bars to report). Data showing response values of zero for quagga mussels mask zero response symbols for zebra mussels. See text for statistical results

about 4 mg L^{-1} (zebra mussels) and 6 mg L^{-1} (quagga mussels) and the percentage increased at higher Ca concentrations, particularly between about 13–18 mg L^{-1} (Fig. 4a). Fertilization appeared independent of Ca at concentrations $\geq$ 18 mg L^{-1}. The binary logistic regression equation relating the probability of mussel fertilization (F) to Ca concentration (Cac) is:

$$F = e^{-4.99862+0.3010\times Cac+0.253881\times Q} \Big/ \left(1+e^{-4.99862+0.3010\times Cac+0.253881\times Q}\right) \times \left(1+e^{-4.99862+0.3010\times Cac+0.253881\times Q}\right)$$

where Q = 1 if quagga mussel or 0 if zebra mussel.

For zygotes, development and survival to the D-veliger stage was only successful in test waters with Ca concentrations $\geq$ 12 mg L^{-1} for quagga mussels and $\geq$13 mg L^{-1} for zebra mussels (Fig. 4b). Here too, survival increased dramatically between

Table 5 Results of binary logistic regression tests of dreissenid mussel reproduction in test waters with different Ca concentrations

Predictor	Coef	SE coef	Z	*P*	Odds ratio	95% Lower	CI upper
Fertilization							
Constant	−4.998632	0.087291	−57.38	0.000			
Ca	0.301010	0.005443	55.30	0.000	1.35	1.34	1.37
Species	0.253881	0.060385	4.20	0.000	1.29	1.15	1.45
Survival to D-veliger							
Constant	−6.01484	0.21869	−27.50	0.000			
Ca	0.32506	0.01229	26.45	0.000	1.38	1.35	1.42
Species	0.50644	0.13974	3.62	0.000	1.66	1.26	2.18
Survival to pediveliger							
Constant	−4.696300	0.274873	−17.09	0.000			
Ca	0.160568	0.012065	13.31	0.000	1.17	1.15	1.20

Main effects include Ca concentrations and mussel species

about 13 and 18 mg L^{-1} and was independent of Ca at higher concentrations. As before, statistical analysis (binary logistic regression) showed that survival to D-veliger was significantly higher at high Ca concentrations and was higher for quagga mussels than zebra mussels (Table 5). The interaction of Ca concentration × species was not significant ($P = 0.714$). The binary logistic regression equation relating the probability of survival to the D-veliger (SD) to Ca concentration (Cac) is:

$$\mathrm{SD} = e^{-6.01484+0.32506\times \mathrm{Cac}+0.50644\times \mathrm{Q}} \Big/ \left(1 + e^{-6.01484+0.32506\times \mathrm{Cac}+0.50644\times \mathrm{Q}}\right)$$

where Q = 1 if quagga mussel or 0 if zebra mussel.

In the simulation of transferring SLR veligers directly into test waters, quagga mussel larvae survived and grew into pediveliger larvae at Ca concentrations ≥ 12 mg L^{-1} and zebra mussels ≥ 13 mg L^{-1} (Fig. 4c). The proportion of surviving larvae increased steadily for both species up to about 23 mg L^{-1}, where it reached maximal values. Again, statistical analysis (binary logistic regression) showed that survival to the pediveliger stage was significantly higher at high Ca concentrations (Table 5) but for this data we could not detect a significant difference among mussel species ($P = 0.225$). Here too, the interaction of Ca concentration × species was not significant ($P = 0.950$). Because this analysis is particularly sensitive to data trends in the region of maximal slope, and because zebra mussel survival was atypically higher within this very region (Fig 4c, Ca 18 mg L^{-1}), the analysis was unable to detect what otherwise appears to be an overall higher survival by quagga mussels. The binary logistic regression equation relating the probability of survival to the pediveliger (SP) to Ca concentration (Cac) is:

$$\mathrm{SD} = e^{-4.69630+0.160568\times \mathrm{Cac}} \Big/ \left(1 + e^{-4.69630+0.160568\times \mathrm{Cac}}\right)$$

Round goby tolerance experiments

Similar to dreissenids, round goby survival during our 63–67 days experiments appeared limited by low SC and Ca levels, and for consistency we relate goby responses to Ca concentrations since this ion is also physiologically important to these fish. Survival of both large and small gobies was ≥50% in water with Ca levels ≥ 8 mg L^{-1} (Fig. 5a). Survival of both size groups was positively related to Ca over concentrations of 0–18 mg L^{-1} but was independent of higher concentrations. Statistical analysis (binary logistic regression) showed that survival increased significantly with Ca concentration (Table 6) but there was no significant difference among goby size groups ($P = 0.199$). Fish mortality in low Ca waters occurred sooner (4 days–2 weeks) than in high Ca waters (>3 weeks) and before dying gobies generally turned darker in color, became lethargic, lost equilibrium and had problems finding and ingesting their food. The binary logistic regression equation relating the probability of goby survival (GS) to Ca concentration (Cac) is:

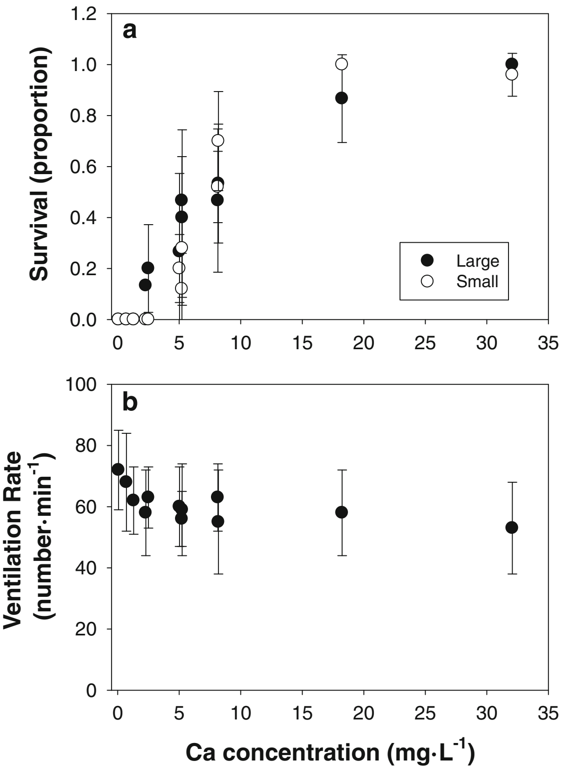

Fig. 5 Survival of round gobies (**a**) and their ventilation rates (**b**) while held for 63–67 days in test waters (see Table 1) spanning a range of dissolved calcium (Ca) concentrations. Survival data are mean (±SD) proportions of 10 sets of 3 large or 5 small gobies alive in each treatment at the end of the experiment. Data showing survival values of zero for small gobies mask zero response symbols for large gobies. A binary logistic regression analysis showed that survival of both large and small gobies increased similarly with Ca concentration ($P = 0.000$). Ventilation data are means (±SD) for 10 sets of 3 large animals in each test water. A Kruskal–Wallis analysis showed that ventilation decreased with Ca concentration ($P = 0.000$)

$$\mathrm{GS} = \mathrm{e}^{-1.933217+0.075812\times \mathrm{Cac}} \Big/ \left(1+\mathrm{e}^{-1.933217+0.075812\times \mathrm{Cac}}\right).$$

Statistical analysis (Kruskal–Wallis ANOVA) showed that the ventilation rates of large gobies fell significantly with Ca concentrations ($H = 50.08$, $df = 11$, $P = 0.000$). Ventilation rates (a potential indicator of physiological stress) were elevated at the lowest two Ca levels but they appeared independent of Ca over higher levels (Fig. 5b). Also, fish held at lower Ca levels often appeared to have larger "tidal volumes", i.e. they ventilated their gills with larger volumes of water, as suggested by larger amplitudes in lateral opercular movement. In sum, both large and small round gobies survived well in the higher Ca waters of the SLR but survival dropped in waters from downstream sections of tributary rivers (5–8 mg L^{-1} Ca) and dropped dramatically in more dilute waters from upstream sections of tributary rivers.

Discussion

Fluvial Lake St. Lawrence appears to have sufficient source populations for secondary spread into NNY inland waters. Our dreissenid density estimates (about 1,000–6,400 individuals m^{-2}) are similar to those reported from the Great Lakes (e.g. 10^2–10^4 m^{-2}; Nalepa et al. 1995; Chase and Bailey 1999; Lozano et al. 2001; Dermott et al. 2003; Haynes et al. 2005) and inland expansion around these lakes has occurred in many locations. Moreover, the adult dreissenids we have sampled in the international section of the SLR are gravid each summer, veliger larvae are common in summer plankton throughout this area, and we have normally observed high settlement of YOY mussels along the riverbed as well as on seaway navigation bouys at the surface (B. Baldwin unpublished data). With all life stages present in the River, and with several boats per day trailered to and from Lake St. Lawrence during summer (Rodger Klindt, New York State Department of Environmental Conservation, unpublished data), there may be sufficient opportunities for spread inland. Indeed such boat movement may have supported the invasion of nearby Black Lake (Fig. 1) back in 2002.

Table 6 Results of binary logistic regression tests of round goby survival in test waters with different Ca concentrations

Predictor	Coef	SE coef	Z	*P*	Odds ratio	95% Lower	CI upper
Constant	−1.933217	0.103095	−18.17	0.000			
Ca	0.075812	0.006383	11.88	0.000	1.36	1.25	1.47

Main effect is Ca concentration

Our dreissenid population densities appear similar to those of other populations along the SLR, from the headwaters down to at least Montreal. In previous years (2002–2005) we have measured similar densities upstream near Cape Vincent and in the 1,000 Islands (B. Baldwin unpublished data) and our Lake St. Lawrence densities, converted to wet mass m^{-2} (using relationships from Baldwin et al. 2002), ranged from about 800 to 4,000 g m^{-2} (mean 1,730 g m^{-2}), which overlaps with several dreissenid population estimates downstream near Montreal (Jones and Ricciardi 2005). Farrell et al. (2010) found lower benthic invertebrate densities in the upper SLR, likely because of differences in sampling technique, but like us, they found dominance of quagga mussels over zebra mussels.

Our population density estimates for round gobies in the SLR (6–32 individuals m^{-2}, excluding most gobies < 3 cm) overlap with those of several other studies from the Great Lakes (which quantified densities as individuals m^{-2}) and compliment the only other study of population levels in the SLR ecosystem. Compared to studies that also used benthic video measurements to quantify mainly adult gobies, our range is generally higher than those from 2002 in western Lake Erie (0.80–7.76 m^{-2}; Johnson et al. 2005) and from 2005 for the Bay of Quinte in northeastern Lake Ontario (0.14–3.88 m^{-2}; Taraborelli et al. 2009). Earlier studies, using traditional census techniques (e.g. strip transects, etc.) documented goby densities of 0.3–9 m^{-2} in a study of Lake St. Clair and tributaries in 1996 (Ray and Corkum 2001) and densities of up to 19 m^{-2} (adults on cobble) and 133 m^{-2} (juveniles on sand) in a study of Lake Michigan in 1994–1996 (Chotkowski and Ellen Marsden 1999). The variability among these studies is likely due to differences in location, time of invasion, and measurement technique. Despite this, we feel our goby populations are comparable to other Great Lake locations from which they have spread to inland tributary systems (Irons et al. 2006; Krakowiak and Pennuto 2008; Kornis and Vander Zanden 2010; Poos et al. 2010). The round goby populations we documented along the riverbed, offshore of the littoral zone, may also be similar to those observed (densities unreported) in profundal zone sites in the upper SLR (Farrell et al. 2010). Certainly the lower densities (up to 400 ha^{-1} or 0.04 m^{-2}) they documented in littoral zone sites (using seining techniques) agree with our general observations (while scuba diving) of increasing densities from the shoreline to deeper census sites along the riverbed. Finally, because we observed high densities of YOY gobies (estimated while diving to be as abundant as 200–400 individuals m^{-2}) and have observed many round goby nests and eggs, we feel SLR populations are plentiful, reproductively active, and capable of dispersing using all life stages.

Despite apparently healthy populations and dispersive life stages of both dreissenids and round gobies in the SLR, we have only confirmed one inland invasion into NNY (zebra mussels into Black Lake) in their nearly 20 year colonization of the SLR. Others have found adult dreissenids in the Grasse river tributary (Harper 2006) downstream of our site R9 (Fig. 1) where there is a man-made canal connecting Lake St. Lawrence to the Grasse. Given the low SC conditions of the Grasse, these adults are likely stressed, non-reproductive, and arose from SLR veligers entering from the canal. Our inland water survey methods, emphasizing shallow locations and traditional sampling techniques, may not have been sufficient to detect these exotics and thus we may have underestimated their secondary spread into NNY ecosystems. It may also be that human vectors of spread, especially of dreissenids, may be low in this region and/or that efforts to educate the public have reduced or prevented transfers from the SLR. However, because round gobies can swim up tributary rivers and eat and grow on non-dreissenid diets of tributary macroinvertebrates (K. Rury unpublished data) it seems likely that environmental conditions must play a key role in limiting their inland spread here in NNY. Based on our laboratory experiments, we feel that the relatively soft waters of our watershed may be a prime limiting factor suppressing their spread. The geology of our NNY watershed resists weathering and dissolution (Chiarenzelli et al. 2011) and thus our tributary rivers and inland lakes have low SC levels that may stress the physiology of these exotics and prevent them from reproducing, growing, and surviving in this region.

In our laboratory bioassays, which lasted about 2 months each, quagga mussels and round gobies showed responses to low SC (and low Ca) waters that were generally similar to the better studied zebra mussel. Along with differences in bioenergetics, growth, shell mass, and colonization patterns among these dreissenid species (Mills et al. 1996, 1999; Claxton et al. 1998; Baldwin et al. 2002, Stoeckmann

2003; Casper and Johnson 2010; USGS 2011a) we often found that quagga mussels survived, grew, and reproduced better than zebra mussels, normally at higher Ca concentrations. Our laboratory findings, using a variety of life stages, may agree with field evidence that suggests a somewhat higher Ca tolerance range for quagga mussels (Zhulidov et al. 2004; Jones and Ricciardi 2005). However, the differences we found relate mainly to the magnitude of responses (e.g. survival, fertilization) and do not show major differences in Ca levels that the two species were sensitive to. Furthermore, we found no decline in zebra mussel responses as Ca concentrations increased. Our study also suggests that the round goby will be similarly restricted from low Ca waters as it colonizes North American ecosystems. Additional, longer term laboratory studies are needed to confirm the importance of Ca or other specific chemical conditions that may limit these exotics and these should be placed in context with more field studies relating colonization level to such environmental factors.

Based on our examination of survival and growth of zebra and quagga mussels it appears that if their benthic life stages (juveniles and adults) are transferred from the SLR to NNY inland waters, both species have the potential to survive well and grow in ecosystems with Ca concentrations $\geq$ 13 mg L^{-1} (Figs. 2, 3). Adults in waters of about 13 mg L^{-1} Ca may also have the capacity to reproduce but fertilization and larval development would be much more successful in waters with Ca concentrations $\geq$ 18 mg L^{-1} (Fig. 4). A Ca concentration threshold of 18–24 mg L^{-1} also seems needed to support high survival of SLR veliger larvae that might be transported into inland waters. Taken together, our results suggest that NNY inland waters, which generally have low SC and Ca, are most at risk from invasion by transported juveniles and adults from the SLR, rather than the more sensitive SLR larvae. However, for dreissenids to establish permanent populations that may expand and significantly impact invaded lakes or rivers they would apparently need Ca concentrations $\geq$ 18 mg L^{-1}. These bioassay observations agree with our surveys of NNY inland waters, in that we only found a permanent invasion and expansion of zebra mussels in Black Lake (average Ca concentrations about 18 mg L^{-1}). Although we feel adequate Ca levels were a major factor supporting this invasion, we also recognize that this inland lake, only 5 miles from the SLR, probably has the highest transfer rate of trailered fishing boats to and from the SLR. Why quagga mussels are not part of this invasion remains unclear.

Our dreissenid bioassays, based on comparative tests of multiple lifestages, should strengthen future modeling efforts based on Ca thresholds needed for colonization and impact by both zebra and quagga mussels. In one of the most recently developed models for dreissenid spread in North America, Whittier et al. (2008) reviewed research on Ca thresholds developed for zebra mussels and assumed similar levels for the little studied quagga mussel. While their four colonization risk categories, related to Ca concentrations (very low [<12 mg L^{-1}], low [12–20 mg L^{-1}], moderate [20–28 mg L^{-1}], and high [>28 mg L^{-1}]), are generally accurate and useful, we would suggest the following refinements (very low [<13 mg L^{-1}], low [13–18 mg L^{-1}], moderate [18–24 mg L^{-1}] and high [>24 mg L^{-1}]) and apply them to both species. Not only do these ranges fit our lab and field data, they agree with most data reviewed in Cohen and Weinstein (2001) as well as more recent studies on Lake George, NY, zebra mussels (Frischer et al. 2005), and zebra and quagga mussels in the SLR near Montreal (Jones and Ricciardi 2005). The latter study is particularly important in that it describes how colonization by the two dreissenids is related to natural gradients in Ca concentrations. Not only does it report differences in apparent minimal thresholds for population development (zebra mussels at >8 mg L^{-1}; quagga mussels > 12 mg L^{-1}) but it (along with Zhulidov et al. 2004) suggests that quagga mussels tolerate higher levels of Ca than zebra mussels. We did not detect clear differences in the Ca levels that zebra and quagga mussels responded to, and did not detect natural Ca gradients in our section of the SLR, but future field or longer term lab studies should examine such possible differences more closely.

Round gobies of the SLR, should they spread up tributary rivers (Fig. 1) or be transferred inland, may survive well in nearby waters with Ca concentrations $\geq$ 18 mg L^{-1} and they might even persist in waters as low as about 8 mg L^{-1} (Fig. 5). Whether gobies at such low Ca levels can remain healthy enough to grow and reproduce successfully is unclear. These gobies should at least be able to eat well since additional laboratory studies of ours confirm that SLR gobies readily consume the non-dreissenid prey (mainly insect larvae) of our NNY tributary rivers (K. Rury unpublished data). Continued surveys of benthic fish communities in NNY tributaries will show whether round gobies expand inland and whether their spread and populations are limited by the lower SC and Ca conditions of our upstream waters. And because Black Lake has adequate levels of Ca ($\geq$18 mg L^{-1}), zebra mussel and insect prey, and relatively high transfer rates of trailered fishing boats, this important recreational fishing lake should get special attention from managers trying to prevent the spread and impacts of exotics such as the round goby. Secondary invasions and associated ecological impacts of other Great Lake tributary systems are occurring in geologic settings where SC (and presumably Ca) is higher (SC $\sim$ 260–900; Irons et al. 2006; Krakowiak and Pennuto 2008; Kornis and Vander Zanden 2010; Poos et al. 2010) but it appears that lower SC waters of our area and elsewhere will remain as uninvaded ecological refuges from these exotic fish. As with dreissenids, modeling efforts on the geographic spread and impact of round gobies might consider the following risk thresholds based on Ca concentrations: low $<$ 8 mg L^{-1}, moderate 8–18 mg L^{-1}, and high $>$ 18 mg L^{-1}. However, because round gobies from Lake Ontario (and presumably our SLR source populations) are genetically distinct from others in North America (Brown and Stepien 2009) future studies should confirm and refine these risk thresholds on round gobies from other locations around the Great Lakes basin.

We are unaware of other studies indicating potential geographic limits to round goby spread based on chemical conditions such as SC or Ca. Being a euryhaline fish, most research has understandably focused on their tolerance of high SC (low to moderate salinity) conditions (Moskal'kova 1996; Charlebois et al. 1997; Karatayev et al. 1998; Reid and Orlova 2002; Corkum et al. 2004; Ojaveer 2006; Ellis and MacIsaac 2009). Even though there is a rich community of native freshwater fish adapted to our region's low SC waters, the physiology of the round goby in North America, a fish well adapted to most other freshwaters here, apparently cannot function properly in these more dilute waters. Because research on dreissenids normally focuses on the Ca component of SC, and because fish need Ca for skeletal system development and maintanence, as well as several other physiological processes, we too have related their survival to Ca levels in our natural waters. However, future work should explore whether other chemical conditions (pH, other ions) are more central to their survival. Past work on the effects of acidification on fish communities have shown how low pH, in association with low Mg, low Ca, and high Al can suppress fish survival and reproduction (e.g. Klauda et al. 1987; Dennis et al. 1995; Marmorek et al. 1998; Warren et al. 2010) so it is doubtful that Ca alone regulates round goby spread.

Assuming our risk thresholds apply to the potential spread of SLR dreissenids and round gobies to inland waters of New York state we can estimate the approximate number of lakes and rivers that could support their populations and face their impacts. First, of the NNY waters we monitor (Table 1) we might expect round gobies to at least survive (Ca $>$ 8 mg L^{-1}) in Lower Lake and the lower sections of the Oswegatchie and Grasse rivers, and perhaps to permanently colonize ($>$18 mg L^{-1}) Black Lake and the Little River. Dreissenids might survive ($>$13 mg L^{-1}) in Lower Lake and could colonize ($>$18 mg L^{-1}) the Little River. Applying our suggested colonization risk thresholds to the larger New York State (NYS) databases on surface waters (S. Kishbaugh, New York State Department of Environmental Conservation, unpublished data) we estimate that <7% of monitored lakes in the SLR basin of NNY, and <5% of those in the Adirondack Park, are at risk of colonization (Table 7). In the nearby watershed of eastern Lake Ontario (a nearby source of closely related dreissenids and round gobies) only one of its river systems (the Oswego river, Ca levels $>$ 30 mg L^{-1}) is colonized by zebra mussels and at risk to quagga mussels and round gobies. Not surprisingly, this NNY region is dominated by low SC/Ca waters draining watersheds whose bedrock geology is resistant to dissolution. By comparison, when the rest of New York state is considered, we estimate that about 300 lakes and rivers are at risk of colonization and ecological impact, should these exotics invade (Table 7). Presently, 42 different NYS lakes and rivers are colonized by zebra mussels, 15 by quagga mussels, and 13 by round gobies, mostly in watersheds south and west of the Adirondack Park (USGS 2011c). Natural resource managers in NYS should continue or expand their efforts to educate the public and prevent the invasion of these exotics in New York state waters.

Table 7 Number of New York State waterbodies (and percent of total) susceptible to colonization by dreissenid mussels and round gobies

Ecosystem type	Region	Number sampled	Ca concentration ranges (mg L^{-1}) related to colonization risk							Database
			Dreissenids				Round gobies			
			<13	13–18	18–24	>24	<8	8–18	>18	
Lotic	Statewide	320	87 (27)	27 (8)	26 (8)	180 (57)	53 (17)	61 (19)	206 (64)	NYS surf waters[a]
Lentic	Statewide	1,150	1,036 (90)	33 (2.9)	33 (2.9)	48 (4.2)	983 (85.5)	85 (7.4)	82 (7.1)	NYS surf waters[b]
Lentic	Statewide	228	125 (55)	29 (13)	28 (12)	46 (20)	91 (40)	63 (28)	74 (32)	NYS CSLAP[c]
Lentic	SLR basin	20	18 (90)	1 (5)	1 (5)	0	13 (65)	6 (30)	1 (5)	NYS CSLAP[d]
Lentic	ADK park	1,490	1,455 (98)	15 (1)	11 (0.7)	9 (0.3)	1,412 (95)	58 (4)	20 (1)	ALSC[e]

Levels of colonization risk by dreissenids (very low, low, moderate, high) and gobies (low, moderate, high) correspond to categories of increasing Ca concentrations. Based on the databases used above, our reported Ca thresholds of 8, 13, 18, and 24 correspond to SC levels of 138, 181, 223, and 274, respectively

Linear regression: SC = Ca concentration $\times$ 8.5178 + 69.84, $R^2 = 0.8707$

[a] New York State (NYS) Department of Environmental Conservation (DEC) surface water survey of streams, specific conductivity (SC), 2009

[b] DEC surface water survey of ponds and lakes, 2009

[c] DEC Citizen Science Lake Assessment Program, 1986–2010

[d] DEC Citizen Science Lake Assessment Program, lakes in the SLR watershed, 2010

[e] Adirondack Lake Survey Corporation, ponds and lakes in the Adirondack park, 1985

Looking more broadly at the US, studies such as Whittier et al. (2008) and Drake and Bossenbroek (2009) illustrate both the large regions of the country that could support dreissenid populations, should they spread, but also regions that may remain as ecological refuges. Our study, which provides more confidence in their dreissenid projections (especially assumptions about quagga mussels) also suggests that large regions of the country remain susceptible to invasion and impacts of the round goby. Because these fish directly impact both the native benthos and economically important recreational fisheries, additional research and management efforts are needed to refine our predictions and prevention of further secondary invasion across North America. Finally, although large regions of the US may remain as refuges to invasion by dreissenids and round gobies, other exotic species with lower SC/Ca tolerances, such as *Limnoperna fortunei* (lower Ca limit of 3 mg L^{-1}; Karatayev et al. 2007) represent a risk to a far greater portion of North America.

Acknowledgments We thank Dr. Michael Schuckers for help with statistical analyses, Carol Cady for help preparing Fig. 1, and Doug Brown, John Ashley, Adam Caswell and Jim Yaeger for assistance with scuba surveys. We are also grateful for access to data on surface water chemistry, shared by Dr. Scott Kisbaugh (NYSDEC Division of Water) and Dr. James McKenna (USGS Great Lakes Science Center). We also thank M. Kornis and an anonymous reviewer for their helpful comments on an earlier version of this paper. This research was supported by an A. C. Walker Foundation North Country Research Fellowship, a grant from the St. Lawrence River Research and Education fund, and additional financial assistance from St. Lawrence University. The US Environmental Protection Agency did not fund or manage the research described here. It has not been subject to Agency review and therefore does not necessarily reflect the views of the Agency. No official endorsement should be inferred.

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