

An invasive benthic fish magnifies trophic cascades and alters pelagic communities in an experimental freshwater system

Katie S. Pagnucco^{1,4}, Yasmina Remmal^{2,5}, and Anthony Ricciardi^{3,6}

¹Department of Biology, McGill University, Montreal, Quebec, Canada, H3A 1B1

²Department of Bioresource Engineering, McGill University, Montreal, Quebec, Canada, H3A 0C4

³Redpath Museum and McGill School of Environment, McGill University, Montreal, Quebec, Canada, H3A 0C4

Abstract: Most studies of the consequences of nonnative fish introductions address only direct effects rather than cascading effects on lower trophic levels or other ecosystem compartments. These trophic cascades have not been studied in comparison to the effects of a functionally similar native species nor with consideration of bottom-up forces (e.g., nutrient supply). The Round Goby (*Neogobius melanostomus*) is an invasive benthic predator that can deplete local populations of grazers, potentially generating substantive increases in benthic algal biomass. Here, we tested, with a factorial experimental design, the influence of Round Gobies on the relative strength of top-down and bottom-up forces in benthic communities by manipulating consumer type (Round Goby or native Logperch (*Percina caprodes*), snails only, or controls where snails and fish were absent), nutrient addition, and the presence of an invasive suspension feeder (Quagga Mussel [*Dreissena bugensis*]) in freshwater mesocosms. We also investigated how these perturbations affect phytoplankton and zooplankton communities. We observed stronger top-down forces in the presence of Round Gobies vs native Logperch, and these forces resulted in reduced grazer abundance and a concomitant increase in benthic algal abundance. However, when Quagga Mussels were present, bottom-up forces dominated. Round Gobies had a significantly greater positive effect on phytoplankton than did native Logperch. Our results highlight the importance of measuring top-down and bottom-up forces in comparison with a trophically similar native species to elucidate the ramifying effects of a nonnative predator on food webs.

Key words: invasive species, food webs, top-down control, bottom-up control, benthic–pelagic coupling, Round Goby, impacts

Although research on biological invasions is focused disproportionately on terrestrial ecosystems (see Puth and Post 2005, Lowry et al. 2012), the need to understand the effects of freshwater invasions is underscored by high invasion rates (Ricciardi 2006, Jackson and Grey 2013) and a disproportionate sensitivity to anthropogenic stressors in lakes and rivers (Ricciardi and Rasmussen 1999, Ricciardi and MacIsaac 2011). The ecological consequences of nonnative freshwater fish introductions have been well documented (see reviews by Moyle and Light 1996, Simon and Townsend 2003, Gozlan et al. 2010, Cucherousset and Olden 2011). However, most studies of the effects of nonnative fishes address solely direct effects rather than indirect interactions, such as cascading effects on other ecosystem compartments, that can alter ecosystem functioning in unpredictable ways. For example, Baxter et al. (2004) found that Rainbow Trout (*Oncorhynchus*

mykiss) introduced to a Japanese stream decreased insect larvae abundances to a point at which insect emergence declined, which led to a 65% reduction in the density of riparian forest spiders that relied on adult aquatic insects as a prey base. Such complex effects of a nonnative species would remain unobserved if researchers limited their investigation to the ecosystem compartment in which the nonnative species resides.

A trophic cascade occurs when an apex predator's influence extends down a food web to affect the abundance of primary producers (Carpenter et al. 1985). Trophic cascades that have been documented for biological invasions have involved stronger indirect effects of nonnative species than similar natives (Flecker and Townsend 1994, Baxter et al. 2004). For example, Flecker and Townsend (1994) compared the effect on a New Zealand stream community of introduced Brown Trout (*Salmo*

E-mail addresses: ⁴katie.pagnucco@mail.mcgill.ca; ⁵yasmina.remmal@mail.mcgill.ca; ⁶tony.ricciardi@mcgill.ca

DOI: 10.1086/685285. Received 5 August 2015; Accepted 9 September 2015; Published online 28 January 2016.
Freshwater Science. 2016. 35(2):654–665. © 2016 by The Society for Freshwater Science.

trutta) with a native galaxiid fish. They showed that Brown Trout reduced the biomass of grazing insects such that algal biomass was greater in the presence of trout than the native fish. In addition to these top-down forces, primary producers may be controlled via growth-limiting resources (e.g., nutrients), termed bottom-up forces. The relative importance of bottom-up vs top-down forces on community-level and trophic-level biomass within and across ecosystem types is a longstanding issue in ecology (Elton 1927, Hairston et al. 1960, Sih et al. 1985, Polis and Strong 1996, Polis 1999), but recent research highlights the interdependence of resource and consumer effects on patterns of primary production (Borer et al. 2006, Burkepile and Hay 2006, Hillebrand et al. 2007).

The effects of nonnative fishes can cascade beyond conventionally defined habitat boundaries and have significant consequences for foodweb dynamics (Winemiller 1990, Polis and Strong 1996, Polis et al. 1997). However, such ramifying effects often are overlooked because researchers typically limit the scope of their studies to one system or even a single system component (e.g., Vilà et al. 2011). In lakes and rivers, benthic and planktonic habitats are physically connected, thereby generating the potential for several modes of interaction via resource use (Blumenshine et al. 1997, Vadeboncoeur et al. 2002). Benthic and pelagic primary productivity are inversely correlated at broad scales because of competing resource needs (Sand-Jensen and Borum 1991, Hansson 1992, Vadeboncoeur et al. 2001). Some evidence has been found of similar compensatory interactions between benthic and pelagic invertebrates (Strayer et al. 1999). Despite the fact that manipulations of resources often have rapid direct effects on both benthic and pelagic communities, such communities typically are studied as though their spatial segregation renders them functionally independent (Boero et al. 1996, Marcus et al. 1998). In a review of 305 studies of benthic primary and secondary production in lake food webs, Vadeboncoeur et al. (2002) found that <6% of studies quantified productivity in both the benthic and pelagic habitats in a lake. Misleading conclusions regarding the ecosystem-level effects of nonnative species may arise when the pelagic or benthic habitat is examined in isolation.

A nonnative fish species that has shown potential to exert cascading effects is the Round Goby (*Neogobius melanostomus*), an invasive benthic predator and the most abundant nonnative vertebrate in the Laurentian Great Lakes–St Lawrence River basin (Dopazo et al. 2008). It has caused the local displacement of native benthic fishes, such as Logperch (*Percina caprodes*), through competition for resources and predation on juveniles (French and Jude 2001, Vanderploeg et al. 2002, Kornis et al. 2012). The rapid spread and voracious appetite of the Round Goby have raised concerns about its long-term effects on native fish populations and ecosystem functioning (Kornis et al.

2012). In addition to causing reductions in the prey base of benthic fishes, Round Gobies can alter the structure of invertebrate communities and thereby indirectly affect benthic algal production (Kuhns and Berg 1999, Lederer et al. 2008). The magnitude of such effects can vary substantially across sites even within a water body (Kipp and Ricciardi 2012). However, previous studies of the ability of Round Gobies to generate trophic cascades were conducted without consideration of bottom-up forces.

In addition, Round Gobies in the Great Lakes–St Lawrence River system rely heavily on mollusks as prey (Kipp et al. 2012, Kornis et al. 2012). Dreissenid mussels are efficient suspension feeders that can reduce phytoplankton abundance and increase water clarity. The continuous conversion of phytoplankton into feces and pseudofeces by mussel filtration activities amplifies the flux of organic matter from the pelagic zone to the benthos (Vanderploeg et al. 2002). The mussels also provide attachment surfaces and biodeposits that support benthic algal growth (Malkin et al. 2008, Ward and Ricciardi 2010). Thus, by reducing the mussel population locally and by recycling nutrients through their feeding activities, Round Gobies may have indirect effects on planktonic communities. No previous researcher has investigated the effects of Round Gobies on phytoplankton or zooplankton.

Here, we factorially manipulated consumer type (either native Logperch or nonnative Round Goby), nutrient addition (N and P), and the presence of Quagga Mussels (*Dreissena bugensis*) in freshwater mesocosms to test the effect of the Round Goby on the relative strength of top-down and bottom-up forces in benthic communities. We also investigated how these perturbations affect planktonic communities. Given that the most damaging invaders often are characterized by an ability to consume and deplete resources rapidly (e.g., Funk and Vitousek 2007, Johnson et al. 2008, Morrison and Hay 2011), we hypothesized that the Round Goby would deplete grazer abundances to a greater extent than would Logperch. We predicted that by depleting benthic grazer densities (e.g., gastropods, amphipods; Kipp and Ricciardi 2012), the Round Goby would elicit a positive response in benthic algal abundances via a trophic cascade, whereas Logperch would not affect benthic algal abundance (see Table 1 for detailed hypothesized effects of each factor on each response variable).

METHODS

Experimental design

We factorially manipulated consumer type, nutrient addition, and the presence of Quagga Mussels in outdoor freshwater mesocosms (114-L plastic containers, 81 × 51.4 × 44.5 cm) at McGill University's Macdonald Campus in Ste-Anne-de-Bellevue, Quebec. Mesocosms were beige and rectangular. We added 5 L of sandbox-grade

Table 1. Hypotheses regarding the effects of the 3 fixed factors manipulated in this experiment and of time on response variables.

Factor	Consumer type	Nutrients	Quagga Mussels	Time
Benthic algal biomass	Increase with Round Goby: trophic cascade via consumption of snails; Kuhns and Berg 1999, Kipp and Ricciardi 2012	Increase with nutrients	Increase with Quagga Mussels: nutrients and attachment surfaces; Vanderploeg et al. 2002	All effects increase over time Alternative: boom–bust cycles lead to oscillations over time
Phytoplankton biomass	Increase with Round Goby: predation relief via consumption of settled algal cells by fish; Roozen et al. 2007 Alternative: decrease from increased competition following increase in benthic algae resource needs; Vadeboncoeur et al. 2001	Increase with nutrients	Decrease with Quagga Mussels: consumption; Gergs et al. 2009	
Zooplankton density	Increase with Round Goby: increased food supply Alternative: decrease if phytoplankton decline from competition with benthic algae	Increase with nutrients	Decrease with Quagga Mussels: zooplankton consumption and food depletion; Mills et al. 1993, Thorp and Casper 2002	
Zooplankton diversity	Increase with Round Goby: predation relief via consumption of mollusks	Increase with nutrients: more nutrients support greater diversity Alternative: decreases as better competitors for nutrients dominate	Decrease with Quagga Mussels: small, pelagic forms consumed; Thorp and Casper 2002	

sand to each mesocosm as sediment to foster natural biogeochemical cycling processes. Both Round Gobies (Ray and Corkum 2001) and Logperch (Smith 1985) prefer cobble substrates, but we chose sand as the substrate for these experiments for logistic reasons. On 6 July 2012, we filled mesocosms with 60 L of dechlorinated tap water mixed with 5 L of water collected from St Lawrence River to inoculate the experimental system with phytoplankton and zooplankton. We covered the mesocosms with 2-mm² vinyl mesh to reduce colonization by macroinvertebrates and to provide shade (mesh reduced light by 20%; KSP, unpublished data). We kept the water level constant by adding dechlorinated tap water as needed throughout the experimental period.

We conducted a 4 × 2 × 2 factorial experiment, in which we manipulated 3 factors: consumer type (control, snails [*Physella* spp.], snails and Logperch, snails and Round Goby); nutrient addition (no nutrients added, N and P added); and Quagga Mussels (present, absent). We replicated each treatment combination 3× for a total of 48 mesocosms. We arranged mesocosms adjacent to each other in a 6 × 8 mosaic plot in which treatments were distributed randomly.

Starting 17 August 2012, we added nutrients as mixtures of ammonium nitrate and potassium phosphate at

weekly intervals to obtain concentrations of 200 µg N/L and 30 µg P/L, levels similar to those used in eutrophication experiments (Rosemond et al. 1993, Kratina et al. 2012). We collected all organisms from the St Lawrence River near Montreal, Quebec. We added 16–25 Quagga Mussels (mean length ± 1 SD: 12.34 ± 2.46 mm, range: 5.73–17.44 mm) and 58–80 physid snails (6.54 ± 1.70 mm, 3.22–10.92 mm) collected on 15 August 2012 to their appropriate mesocosms within 24 h of collection. We collected Logperch (90.5 ± 3.6 mm, 86.0–98.9 mm) and Round Gobies (80.4 ± 3.0 mm, 76.3–86.2 mm) with a seine and added them to the mesocosms on 17 August 2012, which we considered the 1st day of the experiment.

Sampling

We sampled benthic algal biomass, phytoplankton biomass, and total zooplankton density each week for 4 wk (24 August, 31 August, 7 September, 14 September 2012). We sampled benthic algal biomass by scraping mesocosm walls with a 7-cm diameter Whatman GF/F filter affixed to a sponge that sampled an area of 38.5 cm². We collected benthic algal samples from the equivalent quadrat on the equivalent wall of each mesocosm to reduce directionality effects. We stored filters in plastic bags at –20°C pending

analysis. From 9–16 November 2012, we extracted chlorophyll *a* from the filters and analyzed before and after acidification based on standard spectrophotometric methods (Aminot and Rey 2002).

We sampled phytoplankton community biomass by measuring the concentration of chlorophyll *a* in a 30-mL water sample collected from the water column with a syringe. We measured phytoplankton biomass with fluorometry (FluoroProbe, bbe-Moldaenke, Kiel, Germany). We used chlorophyll *a* concentration as a proxy measure of benthic algal and phytoplankton biomass.

We sampled zooplankton abundance and diversity each week of the experiment by collecting 5 L of water from mesocosms and passing it through a 65- μ m-mesh sieve. We rinsed organisms into Falcon tubes and preserved them in 75% ethanol. Zooplankton were counted and identified later to family level. We used Shannon's diversity index (H') to calculate zooplankton diversity for each mesocosm on each sampling occasion.

On the last day of the experiment (14 September 2012), we collected 50-mL water samples from each mesocosm and submitted them to the Université du Québec à Montréal for analyses of total P (TP) and total N (TN). When emptying mesocosms of water, we filtered the substrate through a sieve to collect all remaining snails and Quagga Mussels. We measured the total dry mass of snails and mussels remaining at the end of the experiment to estimate change in mass of each group in each mesocosm.

Top-down vs bottom-up control

To compare the relative strengths of top-down and bottom-up effects on benthic algal abundance, we used a top-down index (TDI) adapted from Rosemond et al. (1993) and calculated it separately for native and nonnative fishes:

$$\text{TDI} = \frac{(\text{fish, no nutrients, no quaggas}) - (\text{snails, no nutrients, no quaggas})}{(\text{snails, nutrients, no quaggas}) - (\text{snails, no nutrients, no quaggas})}, \quad (\text{Eq. 1})$$

where values in parentheses are the treatment means for the Logperch or Round Goby fish treatments. We repeated the calculations for treatments containing Quagga Mussels to assess how their inclusion affected the relative strength of top-down and bottom-up effects. This index is the ratio of the response in the presence of a fish predator without the addition of nutrients to the response in the absence of a fish predator with nutrients added. This equation measures only single-factor effects and not interactive effects. A value of 1 indicates that top-down and bottom-up effects were equivalent, whereas

values >1 or between 0 and 1 indicate that top-down or bottom-up forces were stronger, respectively.

Given that the TDI compares only the direct effects of top-down to bottom-up factors, we also computed the interaction coefficient (IC), an index of the importance of interaction effects on benthic algal abundance, again adapted from Rosemond et al. (1993):

$$\text{IC} = 1 - \frac{\left[\frac{(\text{fish, no nutrients, no quaggas}) - (\text{snails, no nutrients, no quaggas})}{+(\text{snails, nutrients, no quaggas}) - (\text{snails, no nutrients, no quaggas})} \right]}{[(\text{fish, no nutrients, no quaggas}) - (\text{snails, no nutrients, no quaggas})]}, \quad (\text{Eq. 2})$$

where the values in parentheses are treatment means and were repeated for both fish species and with Quagga Mussels added. If the direct effects of fish and nutrients collectively explained the total response in benthic algal biomass, then IC = 0. The IC increases as the importance of the interaction between fish and nutrients increases and approaches 1, at which point the interaction effects account for the entire response. TDI and IC were calculated on $\ln(x)$ -transformed data.

Statistical analyses

We used a 3-way analysis of variance (ANOVA) to test the effects of consumer type (control, snails, snails and Logperch, snails and Round Goby), nutrient addition (no nutrients added, N and P added) and Quagga Mussels (presence vs absence) on the change in snail biomass (final snail mass – initial snail mass) that occurred over the course of the experiment. We used a 2-way ANOVA to test the effects of consumer type and nutrient addition on change in Quagga Mussel biomass.

We examined the effects of consumer type, nutrient addition, and the presence of Quagga Mussels on all 4 response variables (benthic algal biomass, phytoplankton biomass, total zooplankton density, and zooplankton diversity) across the experimental period by means of repeated-measures multivariate ANOVA (MANOVA) with a general linear model. We used Wilks' λ to determine statistical significance. When significant treatment effects were detected, we assessed individual treatment differences with Tukey's Honestly Significant Difference (HSD) multiple-comparison test. Nutrient addition had no significant effects on any response variable and, therefore, was excluded from the final models.

We used 3-way ANOVAs to test the effects of consumer type, nutrient addition, and the presence of Quagga Mussels on N and P measured at the end of the experiment. To achieve normality of residuals and improve homoscedasticity of variances, we $\ln(x)$ -transformed benthic algal biomass, phytoplankton biomass, and total zooplankton density prior to analyses. We used SPSS (version 21;

IBM Statistics, Armonk, New York) for all statistical tests ($\alpha = 0.05$) and SigmaPlot (version 12.5, Systat Software, Chicago, Illinois) to construct figures.

RESULTS

Ability of the Round Goby to generate a trophic cascade

Change in snail biomass was significantly affected by consumer type (3-way ANOVA, $F_{3,36} = 8.78$, $p = 0.001$), but it declined over time across all treatments. Snail biomass declined significantly more in the presence of Round Gobies (mean \pm SE, -2.28 ± 0.26) than in the presence of Logperch (-1.50 ± 0.25 ; Tukey's HSD, $p = 0.034$) or in mesocosms containing snails alone (-1.08 ± 0.08 ; Tukey's HSD, $p = 0.001$; Fig. 1). The abundance of Quagga Mussels at the end of the experiment was not affected by consumer type (2-way ANOVA, $F_{3,24} = 0.486$, $p = 0.697$) or nutrient addition (2-way ANOVA, $F_{1,24} = 0.068$, $p = 0.797$). Quagga Mussels, in turn, did not affect snail biomass (3-way ANOVA, $F_{1,36} = 1.20$, $p = 0.285$).

Benthic algal biomass, phytoplankton biomass, zooplankton density, and zooplankton diversity were measured across 4 levels of consumer type in the presence and absence of Quagga Mussels at 4 time points. Significant multivariate effects were detected for predator type (repeated measures MANOVA, Wilks' $\lambda = 0.235$, $F_{15,94} = 4.341$, $p < 0.001$), Quagga Mussel presence (Wilks' $\lambda = 0.511$, $F_{5,34} = 6.498$, $p < 0.001$), and treatment week (Wilks' $\lambda = 0.325$, $F_{15,24} = 3.317$, $p = 0.004$; Table 2).

Benthic algal biomass was significantly affected by consumer type (univariate between-group analyses, $F_{3,38} = 5.348$,

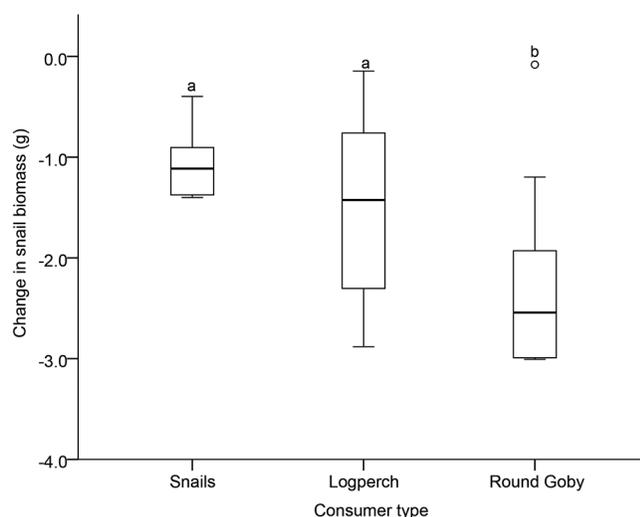


Figure 1. Box plot showing the change in snail mass from the beginning to the end of the experiment for each consumer type. Lines in boxes show medians, box ends show quartiles, whiskers show 10th and 90th percentiles, and circles show extreme data points. Boxes with the same letter are not significantly different (Tukey's Honestly Significant Difference, $\alpha = 0.05$).

$p = 0.004$; Fig. 2) and time ($F_{3,38} = 16.445$, $p < 0.001$). In the absence of Quagga Mussels, the addition of a Round Goby resulted in significantly higher benthic algal biomass than in the snails-only (Tukey's HSD, $p = 0.026$) or Logperch treatment (Tukey's HSD, $p = 0.013$) but did not differ significantly from the control treatment (Tukey's HSD, $p = 0.986$; Fig. 2). Benthic algal biomass was not affected by the presence of Quagga Mussels ($F_{1,38} = 3.000$, $p = 0.091$). Overall, benthic algal biomass increased significantly over time (univariate within-group analyses, $F_{3,38} = 16.445$, $p < 0.001$).

Consumer type significantly affected phytoplankton biomass ($F_{3,38} = 9.552$, $p < 0.001$). Phytoplankton biomass was significantly higher in the presence of Logperch (Tukey's HSD, $p = 0.007$) and Round Gobies (Tukey's HSD, $p < 0.001$) than in the control treatments (Fig. 3). Phytoplankton biomass was highest in the Round Goby treatments, but this abundance was not significantly higher than in Logperch treatments in the absence of Quagga Mussels (Tukey's HSD, $p = 0.214$). Phytoplankton biomass was significantly reduced by the presence of Quagga Mussels across all consumer treatments ($F_{1,38} = 28.81$, $p < 0.001$). Consumer type, Quagga Mussel presence, or time did not affect zooplankton density or diversity.

Top-down vs bottom-up control

The TDI for treatments varied from 0.59 to 11.24 (Table 3). The TDI for Round Gobies (11.24) was nearly an order of magnitude higher than that for Logperch (1.25) in the absence of Quagga Mussels, results that indicate much stronger top-down effects for Round Gobies than the native fish. However, in the presence of Quagga Mussels, bottom-up forces were stronger than top-down forces for both fish treatments (Table 3). The IC varied from 0.26 to 0.82 (Table 3), which indicates that 26–82% of the total effects on benthic algal abundance was explained by the interaction between top-down and bottom-up effects rather than their independent effects alone. The IC was lowest for the Round Goby treatment without Quagga Mussels, which combined with a TDI = 11.24 suggests that benthic algal abundance in Round Goby treatments was primarily subject to top-down control.

Change to nutrient availability

We observed significant effects of consumer treatment on TN at the end of the experiment (3-way ANOVA, $F_{3,48} = 5.98$, $p = 0.002$; Fig. 4A, B). However, this result was driven by the Logperch treatment with nutrients added and no Quagga Mussels (Fig. 4B), in which the TN concentration was significantly higher than in all treatments in which the nutrient was not added (Fig. 4A). TN levels were higher in the presence of fish than in the controls, but the snail, Logperch, and Round Goby treatments were not significantly different (Fig. 4A, B). The

Table 2. Results of multivariate analysis of variance (Wilks' λ) and individual analyses of variance (MS) for effects of consumer type (consumer), Quagga Mussel presence (Quagga), and time on benthic algal abundance, zooplankton density and diversity, and phytoplankton abundance. Only statistically significant main factors were included.

Analysis/variable	Source of variation	df	Wilks' λ or MS	F	P
Multivariate analysis	Consumer	15,94	0.24	4.34	<0.001
	Quagga	5,34	0.51	6.50	<0.001
	Time	15,24	0.33	3.32	0.004
Univariate analyses					
Benthic algal abundance	Consumer	3	4.83	5.35	0.004
	Quagga	1	2.71	3.00	0.091
	Time	3	2.49	16.45	<0.001
	Error	38	0.90		
Zooplankton density	Consumer	3	0.97	1.47	0.238
	Quagga	1	0.28	0.43	0.516
	Time	3	0.75	1.11	0.346
	Error	38	0.66		
Zooplankton diversity	Consumer	3	0.19	1.47	0.239
	Quagga	1	0.03	0.24	0.629
	Time	3	0.05	1.14	0.335
	Error	38	0.13		
Phytoplankton density	Consumer	3	57.00	9.55	<0.001
	Quagga	1	171.90	28.81	<0.001
	Time	3	0.64	0.55	0.464
	Error	38	5.97		

presence of Quagga Mussels had no significant effect on TN (3-way ANOVA, $F_{1,48} = 3.54$, $p = 0.069$). The addition of nutrients had no overall significant effect on TN level measured at the end of the experiment (3-way ANOVA, $F_{1,48} = 0.53$, $p = 0.471$; Fig. 4A, B).

Consumer type significantly affected TP (3-way ANOVA, $F_{3,48} = 6.32$, $p = 0.002$; Fig. 5A, B). This effect was driven by the Logperch treatment with nutrients added and no Quagga Mussels (Fig. 5B), where TP was significantly higher than in all treatments in which P was not added (Fig. 5A). In the absence of added nutrients, TP did not differ among consumer treatments (Fig. 5A). Addition of nutrients led to higher TP concentration (3-way ANOVA, $F_{1,48} = 4.53$, $p = 0.041$; Fig. 5A, B), but this result was driven by the Logperch treatment in which nutrients were added and Quagga Mussels were absent. Quagga Mussel presence had no effect on TP levels (3-way ANOVA, $F_{1,48} = 4.02$, $p = 0.054$; Fig. 5A, B).

DISCUSSION

Ability of the Round Goby to generate a trophic cascade

We have shown that the Round Goby can deplete grazers to a greater magnitude than an intraguild native species (Logperch), thereby triggering a trophic cascade. A trophic cascade might not have occurred had the Round Gobies preferentially consumed dreissenid mussels, which

become increasingly important in Round Goby diets as the fish grows larger (Jude et al. 1995, Ray and Corkum 1997, French and Jude 2001). However, Quagga Mussel survival did not differ between consumer treatments over the course of the experiment, suggesting that neither fish species consumed them. The sizes of Round Gobies and mussels used in our experiments were conducive to mussel predation by gobies (cf. Ray and Corkum 1997), but the presence of alternative prey in the form of smaller thin-shelled mollusks (snails) could have deflected predation from Quagga Mussels (Diggins et al. 2002).

In the absence of Quagga Mussels, snails rapidly reduced benthic algal biomass in mesocosms. The addition of Logperch also resulted in lower benthic algal biomass compared with controls, probably because Logperch did not consume snails at a rate sufficient to allow algal recovery within the experimental period. In contrast, the addition of Round Gobies produced a large increase in benthic algal biomass, eventually resembling algal abundances found in the control mesocosms (which contained neither snails nor fish). In an enclosure experiment, chlorophyll *a* concentrations were 50% greater in the presence vs absence of Round Gobies (Kuhns and Berg 1999). In addition to reducing herbivore densities, Round Gobies probably have positive effects on benthic algae by increasing nutrients in the benthos through excretion of waste products.

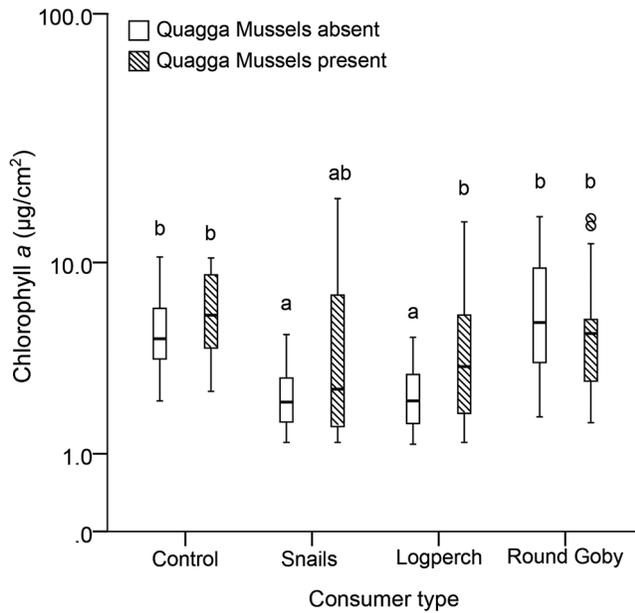


Figure 2. Box plot showing benthic algal biomass (as chlorophyll *a*) for each consumer type when Quagga Mussels were absent or present. Controls lacked consumers (fish and snails). See Fig. 1 for explanation of plot.

Top-down vs bottom-up control

Top-down control implies that predators regulate prey abundance, thereby releasing primary producers, whereas bottom-up control involves primarily abiotic interactions that cause limitation of producers by available resources, such as nutrients or water (Hunter and Price 1992, Power 1992, Meserve et al. 2003). Our experiment indicates that the benthic algal community was under dual control from bottom-up (nutrient limitation) and top-down effects (herbivory constrained by molluscivores). The relative strength of top-down and bottom-up forces was largely governed by consumer type and Quagga Mussel presence. In the absence of Quagga Mussels, the TDIs (see Table 3) indicate that Round Gobies elicited stronger trophic cascades than did Logperch. In contrast, bottom-up forces prevailed for both fish treatments in the presence of Quagga Mussels, which channeled nutrients from the water column to the benthos. These results highlight an increased capacity for Round Gobies to trigger trophic cascades compared with their native counterpart and emphasize the context dependency of top-down and bottom-up control. The TCI index cannot be tested statistically, but these results are supported by results of the repeated-measures MANOVA. Together, they provide strong evidence that Round Gobies are capable of triggering stronger top-down control than a functionally similar native fish.

We observed strong interactive effects between bottom-up and top-down forces in the Logperch treatment without Quagga Mussels, moderate interactive effects for both

fish species in the presence of Quagga Mussels, and weak interactive effects for the Round Goby treatment without Quagga Mussels. These observations suggest that top-down and bottom-up effects alone were less important than their combined effects. In other empirical studies where top-down and bottom-up effects have been tested together, both were found to be significant (Stewart 1987, Power 1990, Steinman 1992, Rosemond et al. 1993, Carpenter et al. 2012). A meta-analysis by Hillebrand (2002) revealed generally strong interactive effects of bottom-up and top-down forces, underscoring the importance of considering both forces when designing an experiment to test trophic cascades.

Cascading effects on phytoplankton

Both the native and nonnative fishes had positive effects on phytoplankton, but the addition of Round Goby generated significantly higher phytoplankton biomass in the presence of Quagga Mussels. In shallow-lake systems, benthivorous fish can stimulate phytoplankton growth by resuspending settled algal cells (Roozen et al. 2007) and by increasing nutrients through excretion (Shormann and Cotner 1997). The quantity and quality of nutrients available in the water column determine phytoplankton demographics, and these effects continue upward through subsequent trophic levels (Wahl et al. 2011). Round Gobies consumed more snails than did Logperch, and this heightened feeding activity may have caused the observed change in phytoplankton by resuspending more nutrients. This result is

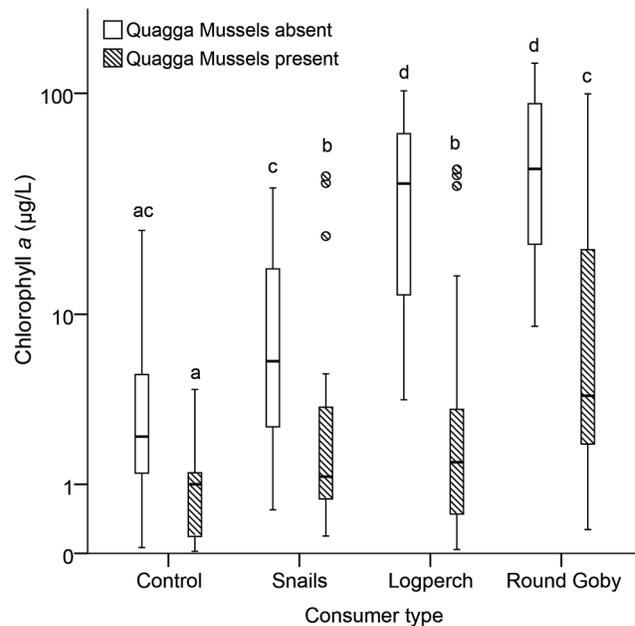


Figure 3. Box plot showing phytoplankton biomass (as chlorophyll *a*) for each consumer type when Quagga Mussels were absent or present. Controls lacked consumers (fish and snails). See Fig. 1 for explanation of plot.

Table 3. Mean benthic algal abundance (measured as chlorophyll *a* [$\mu\text{g}/\text{cm}^2$]) across the sampling period for snail, Logperch, and Round Goby treatments, when nutrients and Quagga Mussels were added or not. Benthic algal abundance data are $\ln(x)$ -transformed. TDI = top-down index, IC = interaction coefficient.

Quagga Mussels	Snail		Logperch				Round Goby			
	No nutrients	Nutrients	No nutrients	Nutrients	TDI	IC	No nutrients	Nutrients	TDI	IC
No	0.87	0.94	0.96	0.96	1.25	0.82	1.74	1.27	11.24	0.26
Yes	1.06	1.40	1.27	1.35	0.62	0.58	1.26	1.71	0.59	0.68

the first evidence published suggesting that Round Gobies can significantly affect phytoplankton abundance.

Quagga Mussels reduced phytoplankton abundances to similar levels across consumer treatments. This result is consistent with field observations of substantive reductions in phytoplankton caused by the high filtration capacity of dreissenid populations (Vanderploeg et al. 2002, Gergs et al. 2009). Phytoplankton biomass also may have been negatively affected by the lower nutrient concentrations that occurred in the presence of Quagga Mussels.

Application of results from a mesocosm experiment across broad spatial scales

A major goal of ecology is to elucidate the mechanisms driving patterns and processes observed in nature. Experiments carried out at the ecosystem scale may be most realistic (Carpenter et al. 1995, Pace et al. 2004), but such experiments often suffer from low replication and limited experimental control (Hurlbert 1984). Therefore, many researchers use mesocosms designed to mimic natural systems while allowing for moderate experimental control, even though such mesocosm experiments have been criticized as being unrealistic simplifications with limited relevance to natural ecosystems (Carpenter 1996, Schindler 1998). In a mesocosm experiment conducted at volumetric scales spanning 5 orders of magnitude, Spivak et al. (2011) showed that algal response to nutrient enrichment did not vary with mesocosm volume or shape, suggesting that results from small-scale experiments examining the direct response of algae to nutrient enrichment may shed light on changes observed in larger, more natural aquatic systems.

Conclusions

Our results demonstrate the ability of a nonnative fish to reduce prey significantly more than a trophically analogous native species, which may be a general pattern for invasive animals (e.g., Dick et al. 2002, 2013, Bollache et al. 2008, Barrios-O'Neill et al. 2014). The most disruptive nonnative species appear to be characterized by their ability to consume and deplete key resources rapidly (Funk and Vitousek 2007, Johnson et al. 2008, Morrison and Hay 2011). We observed stronger top-down forces in the presence of Round Gobies, which resulted in reduced herbi-

vore abundance and a subsequent increase in benthic algal biomass that was not observed with the native Logperch. The presence of another nonnative species, the Quagga Mussel, modified this effect such that bottom-up forces dominated. Several investigators have studied the cascad-

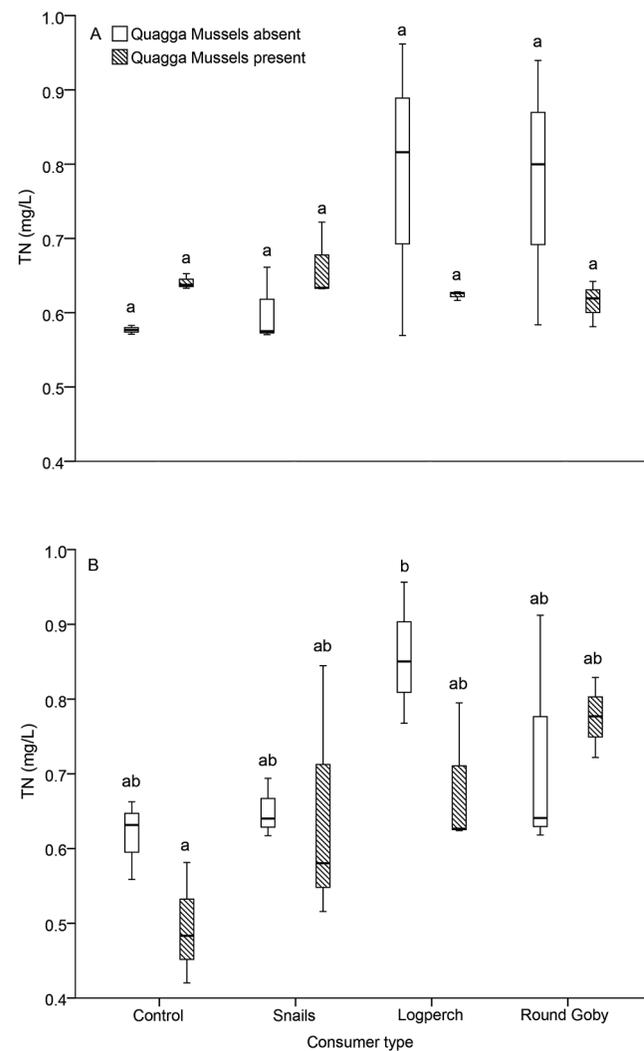


Figure 4. Box plot showing total N (TN) concentration measured at the end of the experiment for each consumer type, when Quagga Mussels were absent or present, and when nutrients were not added (A) or were added (B). Controls lacked consumers (fish and snails). See Fig. 1 for explanation of plot.

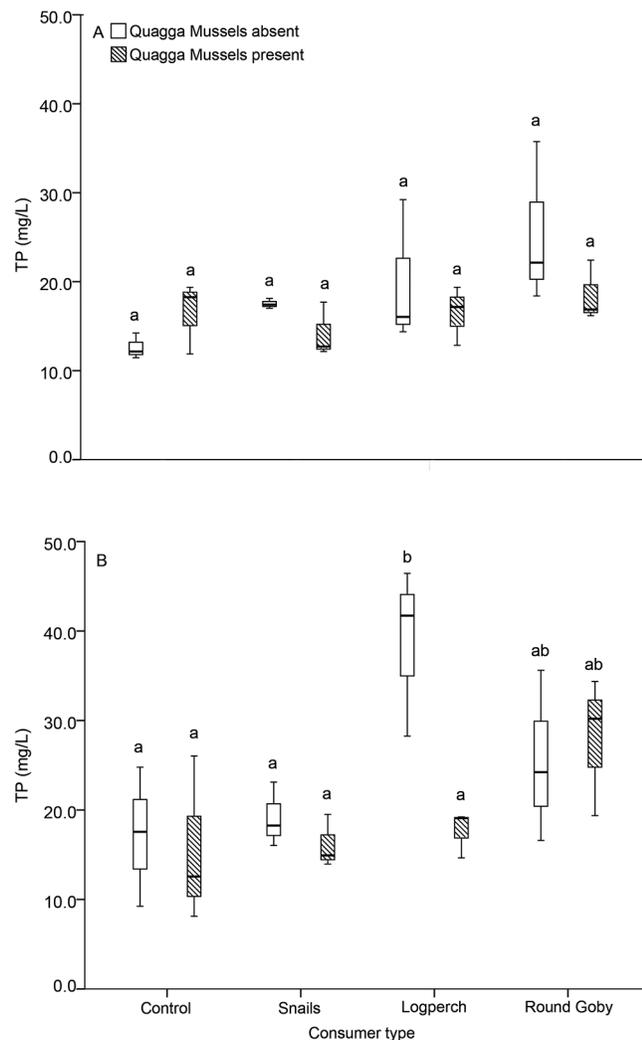


Figure 5. Box plot showing total P (TP) concentration measured at the end of the experiment for each consumer type, when Quagga Mussels were absent or present, and when nutrients were not added (A) or were added (B). Controls lacked consumers (fish and snails). See Fig. 1 for explanation of plot.

ing effects of large-bodied predators, including cichlids (Figueroa and Gianni 2005, Menezes et al. 2012) and salmonids (Flecker and Townsend 1994, McIntosh and Townsend 1996, Parker et al. 2001, Baxter et al. 2004), on lower trophic levels, but our study demonstrates the ability of a small-bodied fish to elicit trophic cascades (see also Preston et al. 2012). The effects of Round Gobies extend beyond the benthos. Round Gobies had significantly greater positive effects than Logperch on phytoplankton biomass. The effects of both predators were altered by the presence of Quagga Mussels. Our results demonstrate the importance of measuring both top-down and bottom-up forces, and making comparisons with effects of a trophically analogous native species, when studying the effects of a nonnative predator on food webs.

ACKNOWLEDGEMENTS

We thank Marie-Claire Chiasson, Katherine Shaw, Karen Wang, and Yinci Yan from McGill University for their laboratory and field assistance. We appreciate feedback on experimental design and collection methods from Patrick Thompson. This study was funded by the National Sciences and Engineering Research Council of Canada and the Canadian Aquatic Invasive Species Network.

LITERATURE CITED

- Aminot, A., and F. Rey. 2002. Chlorophyll *a*: determination by spectroscopic methods. ICES Techniques in Marine Environmental Sciences No. 30. International Council for Exploration of the Sea, Copenhagen, Denmark.
- Barrios-O'Neill, D., J. T. A. Dick, M. C. Emmerson, A. Ricciardi, H. MacIsaac, and M. E. Alexander. 2014. Fortune favours the bold: a higher predator reduces the impact of a native but not an invasive intermediate predator. *Journal of Animal Ecology* 83: 693–701.
- Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663.
- Blumenshine, S. C., Y. Vadeboncoeur, D. M. Lodge, K. L. Cottingham, and S. E. Knight. 1997. Benthic–pelagic links: responses of benthos to water-column nutrient enrichment. *Journal of the North American Benthological Society* 16: 466–479.
- Boero, F., G. Belmonte, G. Fanelli, S. Piraino, and F. Rubino. 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends in Ecology and Evolution* 11:177–180.
- Bollache, L., J. T. A. Dick, K. D. Farnsworth, and W. I. Montgomery. 2008. Comparison of the functional responses of invasive and native amphipods. *Biology Letters* 4:166–169.
- Borer, E. T., B. S. Halpern, and E. W. Seabloom. 2006. Asymmetry in community regulation: effects of predators and productivity. *Ecology* 87:2813–2820.
- Burkpile, D. E., and M. E. Hay. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87:3128–3139.
- Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77: 677–680.
- Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. *Science* 269: 324–327.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 2012. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876.
- Cucherousset, J., and J. D. Olden. 2011. Ecological impacts of nonnative freshwater fishes. *Fisheries* 36:215–230.
- Dick, J. T. A., K. Gallagher, S. Avlijas, H. C. Clarke, S. E. Lewis, S. Leung, D. Minchin, J. Caffrey, M. E. Alexander, C. Maguire, C. Harrod, N. Reid, N. R. Haddaway, K. D. Farnsworth, M. Penk, and A. Ricciardi. 2013. Ecological impacts of an

- invasive predator explained and predicted by comparative functional responses. *Biological Invasions* 15:837–846.
- Dick, J. T. A., D. Platvoet, and D. W. Kelly. 2002. Predatory impact of the freshwater *Dikerogammarus villosus* (Crustacea: Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences* 59:1078–1084.
- Diggins, T. P., J. Kaur, R. K. Chakraborti, and J. V. DePinto. 2002. Diet choice by the exotic Round Goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. *Journal of Great Lakes Research* 28:411–420.
- Dopazo, S. N., L. D. Corkum, and N. E. Mandrak. 2008. Fish assemblages and environmental variables associated with gobiids in nearshore areas of the lower Great Lakes. *Journal of Great Lakes Research* 34:450–460.
- Elton, C. S. 1927. *Animal ecology*. University of Chicago Press, Chicago, Illinois.
- Figueredo, C. C., and A. Giani. 2005. Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). *Freshwater Biology* 50:1391–1403.
- Flecker, A. S., and C. R. Townsend. 1994. Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications* 4:798–807.
- French, J. R. P., and D. J. Jude. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *Journal of Great Lakes Research* 27:300–311.
- Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081.
- Gergs, R., K. Rinke, and K.-O. Rothhaupt. 2009. Zebra mussels mediate benthic–pelagic coupling by biodeposition and changing detrital stoichiometry. *Freshwater Biology* 54:1379–1391.
- Gozlan, R. E., J. R. Britton, I. Cowx, and G. H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76:751–786.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Hansson, L.-A. 1992. Factors regulating periphytic algal biomass. *Limnology and Oceanography* 37:322–328.
- Hillebrand, H. 2002. Top-down versus bottom-up control of autotrophic biomass—a meta-analysis on experiments with periphyton. *Journal of the North American Benthological Society* 21:349–369.
- Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America* 104:10904–10909.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:723–732.
- Hurlbert, S. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Jackson, M. C., and J. Grey. 2013. Accelerating rates of freshwater invasions in the catchment of the River Thames. *Biological Invasions* 15:945–951.
- Johnson, B. M., P. J. Martinez, J. A. Hawkins, and K. R. Bestgen. 2008. Ranking predatory threats by nonnative fishes in the Yampa River, Colorado, via bioenergetics modeling. *North American Journal of Fisheries Management* 28:1941–1953.
- Jude, D. J., J. Janssen, and G. Crawford. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit Rivers. Pages 447–460 in M. Munawar, T. Edsall, and J. Leach (editors). *The Lake Huron ecosystem: ecology, fisheries, and management*. Ecovision World Monograph Series. S. P. B. Academic Publishing, Amsterdam, The Netherlands.
- Kipp, R. M., I. Hébert, M. Lacharité, and A. Ricciardi. 2012. Impacts of predation by the Eurasian Round Goby (*Neogobius melanostomus*) on molluscs in the upper St. Lawrence River. *Journal of Great Lakes Research* 38:78–89.
- Kipp, R. M., and A. Ricciardi. 2012. Impacts of the Eurasian Round Goby (*Neogobius melanostomus*) on benthic communities in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences* 69:469–486.
- Kornis, M. S., N. Mercado-Silva, and M. J. Vander Zanden. 2012. Twenty years of invasion: a review of Round Goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* 80:235–285.
- Kratina, P., H. S. Greig, P. L. Thompson, T. S. Carvalho-Pereira, and J. B. Shurin. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology* 93:1421–1430.
- Kuhns, L. A., and M. B. Berg. 1999. Benthic invertebrate community responses to Round Goby (*Neogobius melanostomus*) and Zebra Mussel (*Dreissena polymorpha*) invasion in southern Lake Michigan. *Journal of Great Lakes Research* 25:910–917.
- Lederer, A., J. Janssen, T. Reed, and A. Wolf. 2008. Impacts of the introduced Round Goby (*Apollonia melanostoma*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and on macroinvertebrate community between 2003 and 2006 in the littoral zone of Green Bay, Lake Michigan. *Journal of Great Lakes Research* 34:690–697.
- Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2012. Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution* 3:182–196.
- Malkin, S. Y., S. J. Guildford, and R. E. Hecky. 2008. Modeling the growth response of *Cladophora* in a Laurentian Great Lake to the exotic invader *Dreissena* and to lake warming. *Limnology and Oceanography* 53:1111–1124.
- Marcus, N. H., F. Boero, B. Marina, and U. Lecce. 1998. Mini-review: the importance of benthic–pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography* 43:763–768.
- McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? *Oecologia* (Berlin) 108:174–181.
- Menezes, R. F., J. L. Attayde, G. Lacerot, S. Kosten, L. C. e Souza, L. S. Costa, E. H. Van Nes, and E. Jeppesen. 2012. Lower biodiversity of native fish but only marginally altered plankton biomass in tropical lakes hosting introduced pi-

- scivorous *Cichla cf. ocellaris*. *Biological Invasions* 14:1353–1363.
- Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutierrez. 2003. Thirteen years of shifting top-down and bottom-up control. *BioScience* 53:633–646.
- Mills, E. L., R. M. Dermott, E. F. Roseman, D. Dustin, E. Mellina, D. B. Conn, and A. P. Spidle. 1993. Colonization, ecology, and population structure of the “quagga” mussel (*Bivalvia: Dreissenidae*) in the lower Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2305–2314.
- Morrison, W. E., and M. E. Hay. 2011. Feeding and growth of native, invasive and non-invasive alien apple snails (*Ampullariidae*) in the United States: invasives eat more and grow more. *Biological Invasions* 13:945–955.
- Moyle, P. B., and T. Light. 1996. Fish invasions in California: do abiotic factors determine success? *Ecology* 77:1666–1670.
- Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell, J. R. Hodgson, M. C. van de Bogert, D. L. Bade, E. S. Kritzberg, and D. Bastviken. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427:240–243.
- Parker, B. R., D. W. Schindler, D. B. Donald, and R. S. Anderson. 2001. The effects of stocking and removal of a nonnative salmonid on the plankton of an alpine lake. *Ecosystems* 4: 334–345.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86:3–15.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–814.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73:733–746.
- Preston, D., J. Henderson, and P. Johnson. 2012. Community ecology of invasions: direct and indirect effects of multiple invasive species on aquatic communities. *Ecology* 93:1254–1261.
- Puth, L. M., and D. M. Post. 2005. Studying invasion: have we missed the boat? *Ecology Letters* 8:715–721.
- Ray, W. J., and L. D. Corkum. 1997. Predation of zebra mussels by Round Gobies, *Neogobius melanostomus*. *Environmental Biology of Fishes* 50:267–273.
- Ray, W. J., and L. D. Corkum. 2001. Habitat and site affinity of the Round Goby. *Journal of Great Lakes Research* 27:329–334.
- Ricciardi, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions* 12:425–433.
- Ricciardi, A., and H. J. MacIsaac. 2011. Impacts of biological invasions on freshwater ecosystems. Pages 211–224 in D. M. Richardson (editor). *Fifty years of invasion ecology: the legacy of Charles Elton*. Wiley–Blackwell, Oxford, UK.
- Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13:1220–1222.
- Roozen, F. C. J. M., M. Lüring, H. Vlek, E. A. J. van der Pouw Kraan, B. W. Ibelings, and M. Scheffer. 2007. Resuspension of algal cells by benthivorous fish boosts phytoplankton biomass and alters community structure in shallow lakes. *Freshwater Biology* 52:977–987.
- Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264–1280.
- Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* 41:137–175.
- Schindler, D. W. 1998. Whole-ecosystem experiments: replication versus realism: the need for ecosystem-scale experiments. *Ecosystems* 1:323–334.
- Shormann, D. E., and J. B. Cotner. 1997. The effects of benthivorous Smallmouth Buffalo (*Ictiobus bubalus*) on water quality and nutrient cycling in a shallow floodplain lake. *Lake and Reservoir Management* 13:270–278.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- Simon, K. S., and C. R. Townsend. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology* 48:982–994.
- Smith, C. L. 1985. *The inland fishes of New York State*. New York State Department of Environmental Conservation, Albany, New York.
- Spivak, A. C., M. J. Vanni, and E. M. Mette. 2011. Moving on up: can results from simple aquatic mesocosm experiments be applied across broad spatial scales? *Freshwater Biology* 56:279–291.
- Steinman, A. D. 1992. Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? *Oecologia (Berlin)* 91:163–170.
- Stewart, A. J. 1987. Responses of stream algae to grazing minnows and nutrients: a field test for interactions. *Oecologia (Berlin)* 72:1–7.
- Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. *BioScience* 49:19–27.
- Thorp, J. H., and A. F. Casper. 2002. Potential effects on zooplankton from species shifts in planktivorous mussels: a field experiment in the St. Lawrence River. *Freshwater Biology* 47:107–119.
- Vadeboncoeur, Y., D. M. Lodge, and S. R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. *Ecology* 82:1065–1077.
- Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. *BioScience* 52:44–54.
- Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1209–1228.
- Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis

- of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- Wahl, D. H., M. D. Wolfe, V. J. Santucci, and J. A. Freedman. 2011. Invasive carp and prey community composition disrupt trophic cascades in eutrophic ponds. *Hydrobiologia* 678: 49–63.
- Ward, J. M., and A. Ricciardi. 2010. Community-level effects of co-occurring native and exotic ecosystem engineers. *Freshwater Biology* 55:1803–1817.
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60:331–367.