

Disentangling the influence of abiotic variables and a non-native predator on freshwater community structure

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Abstract. Cause-and-effect interpretations of the apparent impacts of biological invasions are confounded by the coincident occurrence of non-native species and changes to abiotic factors. Native community structure and function can vary greatly in space and time, owing to abiotic variables that could potentially be affected by non-native species. Here, we sought to determine the relative importance of abiotic variables and an invasive predatory fish, the Eurasian round goby (*Neogobius melanostomus*), on local macroinvertebrate assemblages and benthic algal production in the St. Lawrence River. We used structural equation modeling to evaluate the strength of interaction pathways between hypothesized biotic and abiotic factors driving trophic cascades. Our results indicate that biotic interactions with the round goby drive changes in the abundances of native grazers and non-native dreissenid mussels in the St. Lawrence River. However, the directionality of these effects contradicts previous studies of round goby impacts that emphasized top-down control. We found positive correlations between round goby density and prey (dreissenid and grazer) densities, suggesting complex interactions between round gobies and benthic communities, including strong bottom-up forces. Together with previous studies, our results suggest that, although the interactions between round gobies and benthic communities remain strong, the direction of these interactions varies over space and time. Our results highlight the importance of disentangling the respective roles of biotic interactions and abiotic factors, in order to properly assess the impacts of non-native species as well as the spatiotemporal variability of such impacts.

Key words: benthic macroinvertebrates; bottom-up control; invasive species; multiple drivers; *Neogobius melanostomus*; round goby; St. Lawrence River; structural equation modeling; top-down control.

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INTRODUCTION

Although non-native species invasions are commonly cited as a major cause of ecosystem transformation (e.g., Vitousek et al. 1996, Mack et al. 2000), in many situations it is unclear whether they are drivers of ecosystem change or merely “passengers” along for the ride (Didham et al. 2007). Non-native species often arrive coincidentally with environmental disturbances, con-

founding cause and effect interpretations of impact (MacDougall and Turkington 2005, Shah et al. 2009, Bulleri et al. 2010, HilleRisLambers et al. 2010, White et al. 2013; but see Light and Marchetti 2007 and Hermoso et al. 2011). As such, non-native species may benefit from—or merely be coincident with—an external stressor that suppresses native species. Thus, in the passenger model, the invader’s abundance may be correlated with a decline in a native species

population caused by another external driver such as habitat alteration (Bauer 2012); whereas, in the driver model non-native species are primarily responsible for native species decline, even where habitat alteration has occurred (Light and Marchetti 2007, Hermoso et al. 2011). We may also consider an additive interaction model, in which the invader's impact adds to that of an external stressor and thus both are drivers of native species declines (Hermoso et al. 2011). Abiotic conditions can also affect the functional response of invasive species, with impact scaling disproportionately with invader abundance, leading to synergistic effects (Didham et al. 2007).

The Laurentian Great Lakes basin is the world's most invaded freshwater system, with over 180 non-native species recorded as established (Ricciardi 2006, Pagnucco et al. 2015). Prominent among the non-native species assumed to have caused strong ecological impacts is the round goby (*Neogobius melanostomus*), a benthic Ponto-Caspian fish discovered in the Great Lakes in 1990 (Jude et al. 1992) that has become the most abundant non-native vertebrate in much of the basin (Dopazo et al. 2008, Kornis et al. 2012). Round gobies are voracious and opportunistic predators, feeding on a wide variety of prey items including crustaceans, insects, fish eggs and larvae, and small bivalves (primarily zebra mussels *Dreissena polymorpha* and quagga mussels *Dreissena bugensis*, which are also Ponto-Caspian invaders; Corkum et al. 2004). The establishment of large dreissenid populations in the Great Lakes is thought to have facilitated the rapid expansion of the round goby by providing an abundant resource that few other predators exploit (Jude et al. 1995), but which is a primary food source for adult gobies in their native range (Ghedotti et al. 1995). Dreissenids themselves can cause dramatic changes to benthic communities, by altering the composition and size structure of invertebrates such as gastropods (Ricciardi et al. 1997, Ward and Ricciardi 2007) and stimulating algal growth (Lowe and Pillsbury 1995, MacIsaac 1996, Kuhns and Berg 1999).

In addition to reductions in macroinvertebrate assemblages (Kuhns and Berg 1999, Lederer et al. 2006, Kipp and Ricciardi 2012) and competitive displacement of native fishes (Jude et al. 1995,

Janssen and Jude 2001), round goby invasions are hypothesized to cause changes to ecosystem functioning through trophic cascades (Kuhns and Berg 1999, Kipp and Ricciardi 2012). There is evidence that the round goby enhances benthic algal biomass by substantially reducing grazer populations in the St. Lawrence River, but this effect has been observed at only a subset of invaded sites, likely owing to spatial variation in biotic and abiotic factors (Kipp and Ricciardi 2012).

The “driver-passenger” framework has been used in the past to compare the relative effect of invasive species versus another causal factor (e.g., habitat degradation; Didham et al. 2005, Hermoso et al. 2011). In the present study, we use this framework in a novel way: to tease apart the relative influence of biotic and abiotic interactions on benthic community structure. A previous study by Kipp and Ricciardi (2012) showed that round gobies can transform benthic assemblages and cause indirect positive effects on benthic algae via trophic cascades, but did not assess the role of abiotic factors in driving the observed patterns. Previous work has suggested that site-specific heterogeneity in abiotic factors can have profound effects on an invader's impacts. For example, laboratory experiments showed that intraguild predation of a native amphipod (*Gammarus fasciatus*) and a non-native amphipod (*Echinogammarus ischnus*) on one another varied with conductivity; the non-native species was the dominant predator at high conductivity, and their roles were reversed at low conductivity (Kestrup and Ricciardi 2009). Such studies demonstrate that important insights into an invader's impact can be gained through comparisons of the invader's interactions with co-occurring species across different abiotic conditions, especially within a heterogeneous system.

Here, we used field surveys to determine round goby density, benthic invertebrate density and diversity, and benthic algal abundance across a range of abiotic conditions in the St. Lawrence River. We then used a structural equation modeling (SEM) framework to disentangle causal relationships between biotic and abiotic variables. SEM provides a means to examine possible causal pathways among inter-correlated variables while statistically controlling for other model variables (i.e., to partition

relationships), and examine the likelihood of alternative models given the data at hand (Bollen 1989). We simultaneously tested three alternative models (driver, passenger, and additive) to explain the relationships between the round goby, the benthic macroinvertebrate and algal communities, and abiotic variables. We also evaluated how varying abiotic conditions affected the relationship between round goby density and the benthic macroinvertebrate community, by testing for potential synergistic interactions.

METHODS

In 2011, we sampled 25 sites varying in goby density along a 270-km section of the St. Lawrence River (from Prescott, Ontario to Sainte-Anne-de-Sorel, Quebec; see Appendix A: Fig. A1 for a site map and Table A1 for latitude and longitude coordinates of site locations). Sampling was conducted from 8 July to 24 August, when macroinvertebrate abundance and diversity are generally maximal (Ricciardi et al. 1997). Local round goby densities (m^{-2}) were estimated visually by a diver conducting transect counts at each site (Barton et al. 2005). Estimation of goby densities using direct observational methods have been shown to be significantly more efficient at detecting gobies than traditional trap methods (Johnson et al. 2005). In order to estimate mean goby size at our sites, gobies were collected using a beach seine (mesh size: 0.25 inch); each individual was measured (total length to the nearest mm), and then immediately released. Site-specific round goby densities were similar with both techniques, indicating that collecting gobies using a seine was an effective collection method.

At each site, macroinvertebrates and benthic algae were sampled on the same day that goby counts were conducted. From five random 0.25 m^2 quadrats taken along each of two transects (10 quadrats per site), a diver removed all cobble for subsequent invertebrate and benthic algal analysis. These samples were later pooled within transects, and averaged across site. Transects were placed in 1–2 m of water, end-to-end and parallel to the shoreline. Cobble was rinsed manually with jets of water through the sieve, and macroinvertebrates were retained by a 500- μm sieve were placed in 95% ethanol for

subsequent identification. Each macroinvertebrate was identified to the lowest possible taxon with a dichotomous key under a dissecting microscope (50 \times) and assigned to the primary functional feeding group to which it belonged (Merritt and Cummins 1996). We measured taxonomic diversity using the Shannon diversity index (H'). Owing to inconsistencies in taxonomic resolution, H' was calculated at the family level at each site.

Following collection of macroinvertebrates, benthic algae were scraped from cobble surfaces, and aliquots were filtered, frozen, and analyzed before and after acidification using standard spectrophotometric methods in order to determine chlorophyll-*a* abundance—a proxy for benthic algal abundance (Aminot and Rey 2000). Goby density, dreissenid density, and grazer density were ln-transformed, and benthic algal abundance was arcsine square-root transformed in order to achieve normality.

Eight variables were used to characterize abiotic conditions at each site: dissolved oxygen, conductivity, flow, turbidity, calcium concentration, substrate, distance to outflow, and river width. These variables were selected for their documented importance on benthic algae (Gosselain et al. 2005, Munn et al. 2010, Urrea-Clos et al. 2014), non-dreissenid benthic invertebrates (Rabeni and Minshall 1977, Pinel-Alloul et al. 1996), dreissenids (Mellina and Rasmussen 1994) and round gobies (Pennuto et al. 2010). We measured dissolved oxygen, conductivity, and flow using a YSI Pro2030 (YSI, Yellow Springs, Ohio, USA). From 100-mL water samples, we made five replicate turbidity measurements from each site using a LaMotte 2020we meter (LaMotte Company, Chestertown, Maryland, USA), and five replicate measurements of calcium concentration (mg/L) were derived by titration (LaMotte Total Hardness test kit). We estimated percent cobble cover visually using 10 0.25- m^2 quadrats placed along each goby transect, for a total of 10 samples per site. These were the same quadrats that were used to collect cobble. Measurements of distance to outflow and river width were derived from maps using ArcGIS and Google Earth (see Appendix B: Table B1 for site averages for each environmental variable).

Statistical analyses

All statistics were conducted through SPSS (v. 21, IBM Statistics). We conducted a principal components analysis (PCA) using the correlation matrix from eight abiotic variables to identify the major abiotic gradients for sites across a 270-km stretch of the St. Lawrence River ($n = 25$ sites). We then plotted factor scores for the first two principal components axes for each site, to gain qualitative insight into the total range of variation in abiotic variables among sites across the river. None of the abiotic variables were highly correlated ($r < 0.7$), therefore all eight were retained. Where necessary, we transformed variables to satisfy assumptions of normality.

Two approaches were used to evaluate the influence of round gobies on changes to benthic communities. First, we constructed all possible multiple regression models linking response variables (grazer and benthic algal abundance, and grazer diversity) to a set of predictors (abiotic gradients, goby density, and dreissenid density). An additional predictor, grazer density, was considered for benthic algal abundance. These models included a full model with all the predictors, single models for each predictor, and all possible combinations of multi-variable models. Models were ranked according to their second-order Akaike's information criterion (AIC_c), which should be used when the number of parameters (K) is large relative to the sample size (n), and should be used unless $n/K > 40$ for the model with the largest value of K (Burnham and Anderson 2004). Each model's support was estimated using difference in AIC_c with respect to the top-ranked model (ΔAIC_c). Each model's weight (w_i) can be interpreted as the probability that that model is the best model, given the data and the set of candidate models. We inspected all models having moderate support (i.e., $\Delta AIC_c < 7$ in relation to the best-ranked model; cf. Burnham and Anderson 2002). We did not interpret model-averaged coefficients for predictor variables in order to determine predictor importance, as this practice has recently been shown to be flawed when there is multicollinearity among predictor variables (see Cade 2015).

For our second approach, we tested two separate groups of structural equation models: one group tested the effects of abiotic variables and goby density on benthic grazer density, and

how these effects subsequently affected benthic algal abundance via a trophic cascade (hereafter, the "trophic cascade models"). A second group examined the effects of abiotic gradients and goby density on benthic grazer diversity (hereafter, the "diversity models"). In both groups, we considered dreissenid density (zebra and quagga mussels combined) as a potential driver of grazer density, grazer diversity and benthic algal abundance, and as being driven itself by goby density and abiotic gradients. Correlations between measured variables were analyzed by Pearson's correlation coefficients.

In both the trophic cascade and diversity models, we used SEM to compare three alternative models: additive, driver, and passenger. The additive model included all variables and was used as the baseline for comparison with the other two nested models (driver and passenger). The driver models only considered direct effects of goby density on grazer abundance, grazer diversity, and benthic algal abundance, while abiotic gradients had only indirect effects via round gobies. The passenger model assumed direct effects of abiotic gradients on grazer abundance, grazer diversity and benthic algal abundance, and excluded effects of round gobies.

We used SPSS Amos (v. 21, IBM Statistics) to carry out SEM procedures. We tested each model to ensure that they met the assumptions of multivariate normality. Unlike other multiple regression techniques, path analysis allows a variable to simultaneously be both influenced by other variables and a cause of variation in response variables (Kline 2005). We then applied a path model to test our causal hypotheses of influences on benthic communities in the St. Lawrence River. Standardized partial regression coefficients were calculated for the pathways between each causal variable and the response variables, which included grazer density and benthic algal abundance (trophic cascade models), and grazer diversity (diversity models). Standardization was employed because response variables were measured on different scales. Standardized path coefficients indicate the amount of change in the standard deviation increase in the independent variable. Estimates of path coefficients represent the strength of the path between two variables.

All model parameters were estimated using

maximum likelihood, and the model's goodness-of-fit was performed using a likelihood ratio test. The maximum likelihood procedure minimizes the difference between the observed covariance matrix of variables included in the model and the predicted covariance matrix calculated from the model structure (Shipley 2000). Significance in a path coefficient was determined at the $\alpha = 0.05$ level.

We examined the total effect of each causal variable on each response variable by examining its direct effects (path coefficients) and all indirect effects (the products of path coefficients through mediator variables). We used the bootstrap procedure (1000 samples) to produce confidence intervals (95%) of direct effects, indirect effects, and total effects of each causal variable on each response variable. For both the trophic cascade models and diversity models, additive, driver, and passenger models were ranked according to their Akaike's information criterion (AIC).

In order to assess potential synergistic effects, we tested whether the effects of round gobies were constant along the abiotic gradients or if abiotic conditions enhanced or reduced the effects of round gobies. We used analyses of covariance (ANCOVA) with round goby density as a covariate to test the homogeneity of slopes of the relationship between response variables (grazer density, grazer diversity, benthic algal abundance) and each abiotic gradient (PC 1 and PC 2). In order to use continuous variables as factors, PC gradients were categorized into five equal-sized levels. Significant results of the interaction between round goby density and either PC gradient factor term would imply changes in the per capita impacts of round gobies, whereas non-significant results would suggest numerical responses of benthic communities to round goby density.

RESULTS

The first two axes in the PCA explained 48% of the variation in abiotic variables across all sites measured. The first axis (28%) can be interpreted as a sedimentation gradient, spanning wide, clear, cobble-bottomed sections to narrow, turbid, sandy-bottomed sections of the river (Fig. 1). The second axis (20%) incorporates an ion richness

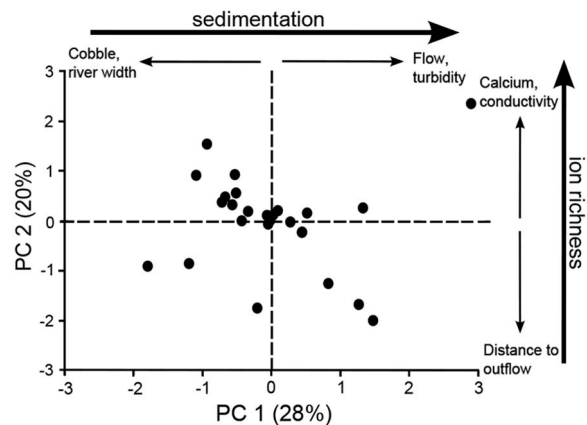


Fig. 1. PCA bi-plot of study sites along the St. Lawrence River. Axis 1 represents a sedimentation gradient and axis 2 represents an ion richness gradient (see text for details on interpretation and Table 2 for loadings of individual variables on each axis). The percent variance explained by each PC is included in parentheses. The variable “distance to outflow” represents the distance from the nearest outflow to the site.

gradient; namely, sites with higher conductivity and calcium concentrations diluted by tributary inputs (thus, ion richness is negatively affected by distance from the nearest tributary outflow; Fig. 1). These two PCs were later used as surrogates for abiotic variables in the analyses. A Pearson correlation coefficient matrix between all measured variables is shown in Table 1.

The top-ranked multiple regression model using grazer abundance as the response variable contained PC 1 and goby density as predictors (Table 2). The second-highest ranked model contained only goby density as the predictor. These were the only two models with $\Delta AIC_c < 2$. Goby density appeared to have the highest relative importance of all predictor variables of grazer abundance, as it was present in 8 of the top 13 models (Table 2). Meanwhile, dreissenid density was present in 7 of the top 13 models, and both PC 1 and PC 2 were present in 6. The top-ranked model when grazer diversity was the response variable contained only goby density as the predictor (Table 2). We were unable to identify a single model among the top five as the best, as each had $\Delta AIC_c < 2$; these models contained various combinations of predictor variables, including PC 1 and dreissenid density,

Table 1. Pearson correlation matrix of the measured variables ($n = 25$).

Variable	PC 1	PC 2	Goby density	Dreissenid density	Grazer density	Algal abundance	Grazer diversity
PC 1	1						
PC 2	0	1					
Goby density	-0.701***	0.084	1				
Dreissenid density	-0.200	0.256	0.383	1			
Grazer density	-0.079	0.071	0.441*	0.344	1		
Algal abundance	-0.445*	0.231	0.593**	0.632**	0.439*	1	
Grazer diversity	0.618**	0.002	-0.646***	-0.031	-0.051	-0.123	1

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

but all included goby density. Goby density again appeared to have the highest relative importance across all predictor variables for grazer diversity, as it appeared in 8 of the top 11 models. PC 1 was present in 7 of the top 11 models, and both PC 2 and dreissenid density were present in 5. The top-ranked model using benthic algal abundance as the response variable included both goby density ($\Sigma w_i = 0.64$) and dreissenid density ($\Sigma w_i = 0.98$) as the predictors (Table 3). This was the only model with $\Delta AIC_c < 2$. It is important to note that, for the most part, regression coefficients for PC 1, PC 2, and dreissenid density were not significant, and

therefore, there is little support for them being important predictors of benthic algal abundance and grazer density and diversity (Table 2).

In our additive structural equation models, PC 1 had significant direct negative effects on both goby and benthic algal abundance (Table 4, Fig. 2a). PC 1 had a significant positive direct effect on grazer density, but this was countered by a significant indirect negative effect with a similar magnitude. PC 1 also had a significant positive effect on both grazer diversity and dreissenid density. PC 2 generally had weak effects on all response variables, except for a significant positive direct effect on dreissenid density. Goby

Table 2. Summary of multiple regression models with moderate support predicting grazer abundance and diversity ($\Delta AIC_c < 7$). K = the number of parameters; AIC_c = second-order Akaike's information criterion; ΔAIC_c = the difference in AIC_c with respect to the top-ranked model; w_i = the Akaike weight.

Model rank	PC 1	PC 2	Goby (m^{-2})	Dreissenid (m^{-2})	K	AIC_c	ΔAIC_c	w_i
Grazer abundance								
1	0.415	...	0.573**	...	4	66.89	0.00	0.31
2	0.333*	...	3	67.48	0.59	0.23
3	0.394	...	0.511**	0.227	5	69.15	2.26	0.10
4	0.455	3	69.73	2.84	0.08
5	0.415	0.007	0.572**	...	5	70.05	3.16	0.06
6	0.319*	0.012	4	70.28	3.39	0.06
7	...	0.031	0.331*	...	4	70.31	3.42	0.06
8	...	-0.012	0.274	0.276	5	72.35	5.46	0.02
9	...	-0.017	...	0.461	4	72.58	5.69	0.02
10	0.397	-0.030	0.512**	0.237	6	72.62	5.73	0.02
11	-0.009	0.452	4	72.73	5.83	0.02
12	-0.072	3	72.73	5.83	0.02
13	...	0.126	3	72.76	5.86	0.02
Grazer diversity								
1	-0.214***	...	3	18.08	0.00	0.22
2	-0.246***	0.147	4	18.46	0.38	0.18
3	0.131	...	-0.138*	...	4	18.52	0.45	0.18
4	0.118	...	-0.175*	0.133	5	19.47	1.40	0.11
5	0.249***	3	19.55	1.40	0.11
6	...	0.023	-0.215***	...	4	20.80	2.72	0.06
7	0.129	0.015	-0.141*	...	5	21.61	3.54	0.04
8	...	0.004	-0.246***	0.147	5	21.62	3.54	0.04
9	0.256***	0.056	4	22.04	3.97	0.03
10	0.249***	0.001	4	22.41	4.34	0.03
11	0.119	0.006	-0.175*	0.135	6	22.97	4.89	0.02

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Summary of multiple regression models with moderate support predicting benthic algal abundance ($\Delta AIC_c < 7$).

Model rank	PC 1	PC 2	Goby density (m ⁻²)	Dreissenid density (m ⁻²)	Grazer density (m ⁻²)	K	AIC _c	ΔAIC_c	w_i
1	2.529**	5.085**	...	4	160.79	0.00	0.32
2	-2.491*	6.061**	...	5	162.78	2.00	0.12
3	-2.472*	5.153**	2.007	5	163.05	2.26	0.10
4	2.257*	4.816**	0.992	5	163.31	2.52	0.09
5	-0.939	...	1.964	5.193**	...	5	163.51	2.72	0.08
6	...	0.597	2.537**	4.860**	...	5	163.62	2.83	0.08
7	6.776***	...	3	164.83	4.04	0.04
8	5.850**	2.037	4	165.26	4.47	0.03
9	-2.528*	0.689	...	5.796**	...	5	165.54	4.75	0.03
10	-1.512	...	1.222	4.864**	1.453	6	165.77	4.98	0.03
11	-2.510*	0.723	...	4.869**	2.022	6	166.06	5.27	0.02
12	...	0.609	2.263*	4.583**	1.002	6	166.47	5.68	0.02
13	-0.991	0.640	1.941	4.957**	...	6	166.63	5.84	0.02
14	3.643***	4	166.71	5.92	0.02
15	...	0.551	...	6.573**	...	4	167.47	6.68	0.01

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

density had significant positive direct effects on dreissenid density and grazer density, and a significant positive indirect effect on benthic algal abundance. Dreissenid density had a significant positive direct effect on benthic algal abundance.

In our driver models, PC 1 had a significant direct negative effect on goby density, and a significant indirect negative effect on benthic algal abundance (Table 4, Fig. 2b). PC 1 also had a significant indirect positive effect on grazer density. Goby density had significant positive direct effects on dreissenid density and grazer density, a significant positive indirect effect on benthic algal abundance, and a significant negative direct effect on grazer diversity. Dreissenid density had a significant direct positive effect on benthic algal abundance.

In our passenger models, PC 1 had significant direct negative effects on goby and dreissenid densities, and benthic algal abundances (Table 4, Fig. 2c). PC 1 also had a significant direct positive effect on grazer diversity. PC 2 had a significant direct positive effect on dreissenid density. Dreissenid density had a significant direct positive effect on benthic algal abundance.

The additive and driver models were consistent with the data for grazer density and benthic algal abundance, as the difference in the observed and expected covariation matrices was not statistically significant ($P = 0.699$ and 0.196 for the additive and driver models, respectively; Fig. 2). The goodness-of-fit test indicated the passenger model, in which the effect of round goby abundance on native assemblages was not

included, was inconsistent with the data for grazer density, since the difference in the observed and expected covariation matrices was statistically significant ($P = 0.043$). The same pattern was observed when considering grazer diversity as the response variable (additive model: $P = 0.356$; driver model: $P = 0.413$; passenger model: $P = 0.071$). The top-ranked trophic cascade model in the SEM analyses was the driver model (AIC = 66.0; Fig. 2b). The additive model (AIC = 80.9; Fig. 2a), which included both measures of abiotic variables (sedimentation and ion richness) as predictors, and the passenger model (AIC = 81.6; Fig. 2c), which omitted round gobies as a predictor, performed poorly by comparison. Similarly, when considering grazer diversity as the response variable, the driver model was the top ranked model (AIC = 45.9; Fig. 2b), while the additive model (AIC = 58.9; Fig. 2a) and the passenger model (AIC = 59.1; Fig. 2c) performed poorly.

There were no significant interactions between round goby density and abiotic gradients (PC 1 and PC 2) for any of the four response variables (dreissenid density, grazer density, grazer diversity, and benthic algal abundance; Table 5). In all cases, we observed positive correlations between round goby density and total grazer abundance, dreissenid abundance, and benthic algal abundance, and negative correlations between round goby density and grazer diversity.

Table 4. Influences of causal variables on response variables, as calculated using structural equation modeling. Standardized path coefficients are listed for the direct effects for each causal variable. Standardized indirect effects are the products of the path coefficients via moderating variables. Standardized total effects are the sum of direct and indirect effects. Bias-corrected 95% confidence limits and *P*-values were estimated from 1000 bootstrap samples.

Model and measured variable	Causalvariable	Direct effects	Indirect effects	Total effect
Additive				
Goby	PC 1	-0.70 (-0.87, -0.22)*	...	-0.70 (-0.87, -0.22)*
Drei.	PC 1	0.11 (-0.65, 0.69)	-0.31 (-0.85, 0.16)	-0.20 (-0.48, 0.16)
Gra. den.	PC 1	0.43 (0.08, 1.10)*	-0.51 (-1.24, -0.07)*	-0.08 (-0.41, 0.28)
Algae	PC 1	-0.34 (-0.53, -0.08)*	-0.11 (-0.28, -0.11)	-0.45 (-0.68, -0.03)*
Gra. div.	PC 1	0.32 (0.16, 0.72)*	0.30 (-0.01, 0.87)	0.62 (0.14, 0.78)*
Goby	PC 2	0.08 (-0.24, 0.32)	...	0.08 (-0.24, 0.32)
Drei.	PC 2	0.22 (0.02, 0.84)*	0.04 (-0.08, 0.34)	0.26 (0.04, 0.72)*
Gra. den.	PC 2	-0.32 (-0.43, 0.43)	0.10 (-0.12, 0.36)	0.07 (-0.44, 0.52)
Algae	PC 2	0.10 (-0.10, 0.32)	0.13 (-0.15, 0.34)	0.23 (-0.13, 0.46)
Gra. div.	PC 2	0.04 (-0.26, 0.37)	-0.04 (-0.21, 0.05)	0.26 (-0.31, 0.36)
Drei.	Goby	0.44 (0.12, 1.00)*	...	0.44 (0.12, 1.00)*
Gra. den.	Goby	0.68 (0.19, 1.28)**	0.08 (-0.06, 0.56)	0.76 (0.41, 1.34)**
Algae	Goby	...	0.39 (0.01, 0.75)*	0.39 (0.01, 0.75)*
Gra. div.	Goby	-0.42 (-0.92, -0.09)*	...	-0.42 (-0.92, -0.09)*
Gra. den.	Drei.	0.18 (-0.14, 0.56)	...	0.18 (-0.14, 0.56)
Algae	Drei.	0.45 (0.20, 0.68)**	0.04 (-0.03, 0.22)	0.50 (0.26, 0.69)**
Algae	Gra. den.	0.25 (-0.09, 0.54)	...	0.25 (-0.09, 0.54)
Driver				
Goby	PC 1	-0.70 (-0.87, -0.22)*	...	-0.70 (-0.87, -0.22)*
Drei.	PC 1	...	-0.27 (-0.45, -0.08)	-0.27 (-0.45, -0.08)
Gra. den.	PC 1	...	-0.31 (-0.51, -0.11)	-0.31 (-0.51, -0.11)
Algae	PC 1	...	-0.22 (-0.37, -0.08)*	-0.22 (-0.37, -0.08)*
Gra. div.	PC 1	...	0.45 (0.06, 0.71)*	0.45 (0.06, 0.71)*
Goby	PC 2	0.08 (-0.24, 0.32)	...	0.08 (-0.24, 0.32)
Drei.	PC 2	...	0.03 (-0.08, 0.14)	0.03 (-0.08, 0.14)
Gra. den.	PC 2	...	0.04 (-0.09, 0.17)	0.04 (-0.09, 0.17)
Algae	PC 2	...	0.03 (-0.07, 0.12)	0.03 (-0.07, 0.12)
Gra. div.	PC 2	...	-0.05 (-0.22, 0.12)	-0.05 (-0.22, 0.12)
Drei.	Goby	0.38 (0.12, 0.60)**	...	0.38 (0.12, 0.60)**
Gra. den.	Goby	0.36 (0.02, 0.64)*	0.08 (-0.04, 0.33)	0.44 (0.15, 0.65)**
Algae	Goby	...	0.32 (0.14, 0.50)*	0.32 (0.14, 0.50)*
Gra. div.	Goby	-0.65 (-0.83, -0.15)*	...	-0.65 (-0.83, -0.15)*
Gra. den.	Drei.	0.21 (-0.13, 0.59)	...	0.21 (-0.13, 0.59)
Algae	Drei.	0.54 (0.33, 0.73)**	0.05 (-0.03, 0.22)	0.60 (0.41, 0.74)**
Algae	Gra. den.	0.25 (-0.07, 0.51)	...	0.25 (-0.07, 0.51)
Passenger				
Goby	PC 1	-0.70 (-0.87, -0.22)*	...	0.25 (-0.07, 0.51)
Drei.	PC 1	-0.20 (-0.48, 0.16)	...	-0.20 (-0.48, 0.16)
Gra. den.	PC 1	-0.01 (-0.41, 0.34)	-0.07 (-0.28, 0.03)	-0.08 (-0.41, 0.28)
Algae	PC 1	-0.34 (-0.53, -0.08)*	0.11 (-0.28, 0.11)	-0.45 (-0.68, -0.03)*
Gra. div.	PC 1	0.62 (0.14, 0.78)*	...	0.62 (0.14, 0.78)*
Goby	PC 2	0.08 (-0.24, 0.32)	...	0.08 (-0.24, 0.32)
Drei.	PC 2	0.26 (0.04, 0.82)*	...	0.26 (0.04, 0.82)*
Gra. den.	PC 2	-0.02 (-0.51, 0.44)	0.09 (-0.02, 0.28)	0.07 (-0.44, 0.52)
Algae	PC 2	0.10 (-0.10, 0.32)	0.13 (-0.15, 0.34)	0.23 (-0.13, 0.46)
Gra. div.	PC 2	0.00 (-0.31, 0.36)	...	0.00 (-0.31, 0.36)
Gra. den.	Drei.	0.35 (-0.01, 0.68)	...	0.35 (-0.01, 0.68)
Algae	Drei.	0.45 (0.20, 0.68)**	0.09 (-0.01, 0.28)	0.54 (0.20, 0.72)**
Algae	Gra. den.	0.25 (-0.09, 0.54)	...	0.25 (-0.09, 0.54)

Note: Goby = Goby density; Drei. = Dreissenid density; Gra. den. = Grazer density; Algae = Benthic algal density; Gra. div. = Grazer diversity.

P* < 0.05, *P* < 0.01, ****P* < 0.001.

DISCUSSION

Our results suggest that biotic interactions involving the round goby are an important

driver of changes in native grazer and dreissenid mussel abundance, and cause indirect effects on benthic algae in the St. Lawrence River. We detected few direct effects of abiotic gradients on

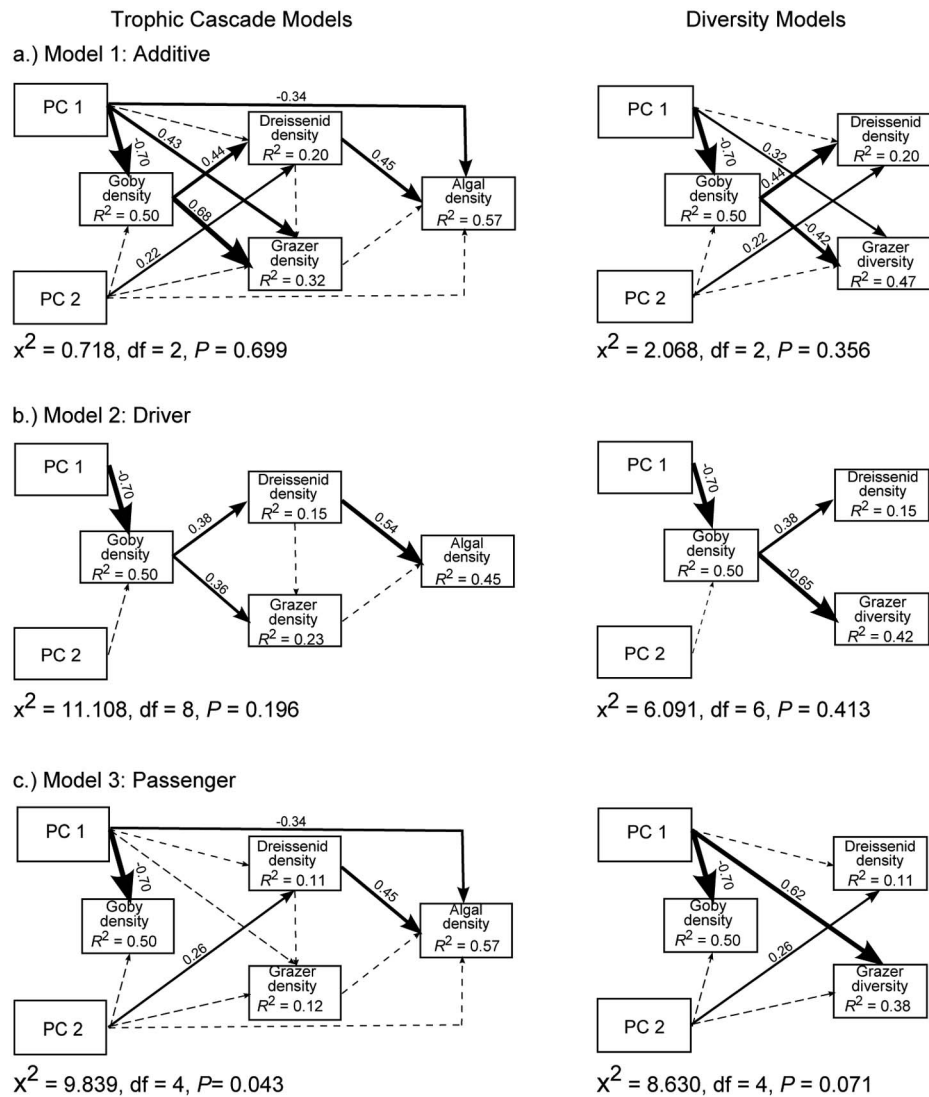


Fig. 2. Scheme of different structural equation models testing alternative pathways of round gobies and abiotic gradients on native benthic communities. In the driver model (b) we assumed that goby density is driving changes in benthic communities (measured using grazer density, benthic algal abundance, and grazer diversity), whereas in the passenger model (c) abiotic gradients have the leading role. The additive model (a) includes all potential paths between the variables considered. Standardized coefficients based on the correlation matrix for each path are shown. Dotted lines represent nonsignificant effects, and line thickness is proportional to their relative weight. The chi-square statistic (testing significant differences between the observed and expected covariance matrices), degrees of freedom (df), and P (based on likelihood-ratio test) are also shown. Significant differences ($P < 0.05$) indicate poor fit between the tested model and the observed data. R^2 values are displayed for all endogenous variables.

invertebrate and benthic algal abundances, whereas the relationship between round gobies and invertebrates was consistent. SEM indicated that round goby density is a more influential

driver of change to benthic communities than the abiotic variables considered in this study, but the directionality of biotic interactions was the opposite of what we expected based on previous

Table 5. Results of partial ANCOVAs testing the effect of goby density on dreissenid density, grazer density, benthic algal abundance, and grazer diversity.

Factors	F	df	P
Dreissenid density			
Goby	0.02	1	0.880
PC 1	2.03	4	0.140
Goby × PC 1	(1.64)	(4)	(0.217)
Goby	6.23	1	0.025
PC 2	2.19	4	0.119
Goby × PC 2	(1.40)	(4)	(0.280)
Grazer density			
Goby	5.93	1	0.025
PC 1	1.44	4	0.260
Goby × PC 1	(−0.091)	(4)	(0.482)
Goby	3.61	1	0.077
PC 2	0.13	4	0.970
Goby × PC 2	(0.38)	(4)	(0.818)
Benthic algal abundance			
Goby	0.26	1	0.618
PC 1	0.38	4	0.817
Goby × PC 1	(1.38)	(4)	(0.289)
Goby	9.09	1	0.009
PC 2	1.31	4	0.311
Goby × PC 2	(0.79)	(4)	(0.550)
Grazer diversity			
Goby	0.27	1	0.614
PC 1	0.46	4	0.767
Goby × PC 1	(0.39)	(4)	(0.810)
Goby	0.05	1	0.831
PC 2	2.10	4	0.139
Goby × PC 2	(0.76)	(4)	(0.570)

Notes: Abiotic gradients were categorized into factors (see *Methods* for details). When nonsignificant ($P > 0.05$), interaction terms (in parentheses) were removed from final models.

published studies of round goby impacts and from food webs under top-down control (see *Mechanisms leading to positive interactions* below).

The distributions of round gobies and dreissenid mussels are limited by low levels of dissolved ions (Baldwin et al. 2012). In laboratory bioassays, round gobies show moderate survival in waters with calcium ion concentrations of at least 8 mg/L and high survival at 18 mg/L; zebra and quagga mussels showed limited reproductive success, growth, and survival in waters with calcium ion concentrations of 13 mg/L, and these measures improved dramatically in waters of 18 mg/L (Baldwin et al. 2012). Similarly, a field study found that zebra mussel and quagga mussel biomasses were limited by low calcium (<20 mg/L) in areas of the St. Lawrence River system (Jones and Ricciardi 2005). While we observed a positive correlation between ion richness and dreissenid density, there was no

significant effect on goby density across our sites, in which calcium ion concentrations ranged from 21 to 36 mg/L (Appendix B: Table B1), which are well-within the tolerance ranges for both dreissenids and round gobies. Ion richness within the range encountered at our study sites would not be expected to have a significant effect on the abundance of gobies and dreissenids. Instead, round gobies and benthic algae may have been limited by availability of cobble. Round gobies tend to be more abundant amongst rocky substrate compared to depositional environments, owing to a preference for interstitial habitat (Ray and Corkum 2001). Benthic algal abundance declined with increasing sedimentation. Although some (epipellic) types of algae colonize fine sediments, few macroscopic species thrive in unstable depositional environments (Stevenson et al. 1996). We found weak positive and negative effects of sedimentation on dreissenid density, suggesting that dreissenids were not limited by substrate. Although zebra mussels are generally more abundant on hard substrates (Mellina and Rasmussen 1994, Nalepa et al. 1995), quagga mussels—which dominated our sites—can thrive on soft substrates (Mills et al. 1993), and both species can attain high biomasses (>1 kg/m²) on silt and mud (Jones and Ricciardi 2005).

Although grazer density was not correlated with either ion richness or sedimentation, the latter had a significant positive effect on grazer diversity. In cobble areas, benthic grazers are potentially vulnerable to intense predation from macroinvertebrates able to exploit these interstitial habitats as refugia against fish predation. However, as percent cobble diminished and sites transitioned to predominantly fine sediment habitats downstream along the river, habitat complexity and refugia diminished. Lack of refugia renders benthic macroinvertebrate predators more vulnerable to predation by fish and other tertiary consumers, such as cormorants (Johnson et al. 2015), thereby suppressing predation on benthic grazers and allowing a greater diversity of grazers to proliferate (Peterson 1979, Wilson 1990, Power 1992).

Dreissenid density had a strong positive effect on benthic algal abundance. This result is consistent with published observations of the capacity for dreissenids to divert nutrients from

the water column to the benthos (Holland et al. 1995, Kuhns and Berg 1999, Hecky et al. 2004) and to stimulate benthic algal growth, as well as providing substrate on which algae can grow.

Mechanisms leading to positive interactions

Positive interactions between round gobies and both dreissenids and grazers are uncommon (see Kipp and Ricciardi 2012). Dreissenids become increasingly important in round goby diets as the fish grow larger (Jude et al. 1995, Ray and Corkum 1997, French and Jude 2001, Janssen and Jude 2001, Lederer et al. 2006). In lab experiments, a broad range of sizes of adult round gobies consume small zebra mussels (<10 mm in length), but only large fish (>80 mm) consume larger zebra mussels (10.0–12.9 mm) when all prey sizes were presented (Ray and Corkum 1997). Similarly, Ghedotti et al. (1995) reported that zebra mussels larger than 12 mm could not be consumed by a round goby of <70 mm length. The round gobies collected in our study were relatively small and included juveniles: the average goby size across all sites was 58 mm and site averages ranged from 29 to 82 mm. Meanwhile, the dreissenids measured at the same sites were generally large: site averages for shell lengths ranged from 12 to 24 mm, which would be unavailable to most gobies at our study sites. As such, round gobies did not seem to have a negative effect on dreissenids, likely because the size of dreissenids present at our site were beyond the gape capacity of the fish. It is possible that round gobies were consuming smaller dreissenids uniformly everywhere, such that we did not detect differences in dreissenid density across sites. Round gobies have been known to consume molluscs to the extent that populations shift in size-dominance (Kipp et al. 2012).

Furthermore, the presence of alternative prey might reduce predation pressure on dreissenids. Diggins et al. (2002) suggested that the large contribution of dreissenids to the round goby diet in the Great Lakes may not necessarily reflect a dietary preference, but rather higher encounter rates compared with motile prey such as amphipods. Thus, the impact of round gobies on dreissenids may be delayed in the vicinity of the invasion front, if non-dreissenid prey are available and initially preferred. Preference for molluscs may vary with time since invasion for

reasons other than changes in predator size, as suggested in a study of the diet of round gobies across different stages of establishment throughout the Danube River: Brandner et al. (2013) showed that, whereas gobies shifted from insects and crustaceans to a mollusc-dominated diet upon reaching 100 mm in length, the pioneering population exhibited a less pronounced diet shift at a larger size (125 mm). In our study, if round gobies were unable to consume most available dreissenids, they could have had a net positive effect on dreissenid abundance by resuspending nutrients through disturbance of the substrate.

Round gobies had positive effects on grazer density, but negative effects on grazer diversity. Fish may preferentially prey on large predatory invertebrates, thus releasing smaller non-predatory invertebrates such as grazers from invertebrate predation, leading to increases in abundance. However, this is an unlikely scenario for our study, since predatory invertebrates were relatively uncommon at our study sites, and have never been shown to be a prominent component of round goby diets (Phillips et al. 2003, Barton et al. 2005, Campbell et al. 2009, Raby et al. 2010). In Lac Saint-Louis in 2009, gobies were not found to consume any predatory macroinvertebrates except certain caddisflies (Kipp et al. 2012).

A study by Diehl (1992) investigating the effects of yellow perch (*Perca flavescens*) on invertebrate communities found that while perch had a net negative effect on non-molluscan herbivore abundance, they had no effect on biomass. Diehl (1992) suggested that perch fed selectively on competitively dominant herbivorous species, thus allowing for a compensatory increase in the biomass of species not consumed by perch. In contrast, we found that gobies had a positive effect on grazer density, but we did not measure biomass. Conversely, it is possible that round gobies fed on benthic grazers in such a way that allowed competitively-dominant grazer species to increase in abundance to compensate for declines in less competitive grazers; consequently, we observed a net increase in overall density of grazers, but a decline in evenness reflected in lower Shannon diversity.

In their study of the effects of native juvenile creek chubs (*Semotilus atromaculatus*) on benthic invertebrates, Harvey and Hill (1991) found that fish reduced total biomass, but not the total

number of invertebrates, owing to preference for large taxa. Where fishes tend to select larger prey, reductions in total prey number are difficult to detect, in part because larger taxa are also generally rare, but account for a substantial proportion of total invertebrate biomass. Similarly, in their study investigating the effects of the round goby on molluscs in the St. Lawrence River, Kipp et al. (2012) found that mean gastropod size declined following round goby invasion, presumably due to predation. Kipp and Ricciardi (2012) found that areas with dense populations of round gobies were dominated by smaller taxa, such as chironomids. If round gobies prefer larger prey in general, they could conceivably cause shifts in benthic invertebrate populations towards dominance of smaller taxa, leading to reductions in benthic invertebrate biomass, but not necessarily density.

*Evidence of bottom-up control
in an invader-dominated food web*

Although we have proposed some mechanisms that could lead to the observed patterns, we suggest that bottom-up rather than top-down control is the most parsimonious explanation for the observed positive relationships between round goby density and that of dreissenids and grazers. SEM is a powerful technique for teasing apart interactions between multiple, independent and dependent variables, but its construction relies on assumptions concerning the direction of causation. In our study, we assumed that each trophic level would be affected by the trophic level immediately above it; but it is possible that organisms were instead experiencing a net effect from the trophic level below. The biomass and composition of primary producers is affected by both resource supply (bottom-up) and by consumption from herbivores (top-down). Benthic algal biomass can be efficiently reduced by grazers (Feminella and Hawkins 1995), but can also be profoundly affected by changes in light and nutrient supply (Rosemond et al. 1993). Changes in resource supply may regulate benthic algal abundance such that its influence on higher trophic levels overwhelms any top-down effects, thus explaining the positive relationships between trophic components in this study. It may be that grazers tend to gravitate towards habitats with an abundance of benthic algae, and round

gobies are in turn attracted to habitats with an abundance of food resources—that is, grazers and dreissenids (see Fig. 3 for a concept map of top-down and bottom-up interactions between biotic components and abiotic gradients).

We were unable to conclude that the consumption of grazers by round gobies could lead indirectly to an increase in benthic algal abundance; nevertheless, we observed a positive indirect effect of round goby density on benthic algal abundance. This “apparent trophic cascade” was the result of positive correlations between round goby density and dreissenid density, and between dreissenid density and benthic algal abundance, rather than round gobies causing reductions in grazer densities.

*The context-dependence of round goby
impacts within the St. Lawrence River*

Our study showed that the changes in abundances of benthic grazers, dreissenids, and benthic algae were better explained by their interactions with one another and with varying density of round gobies than with abiotic variables. We found that benthic algal abundance was higher in the presence of round gobies, a pattern that has previously been shown to be the result of a trophic cascade mediated by a decline in grazers as a result of goby consumption (Kipp and Ricciardi 2012). However, in our study, this pattern was not the result of a trophic cascade; instead, it was likely the result of bottom-up control. The capacity of round gobies to exert strong top-down control in the St. Lawrence River has been shown by Kipp and Ricciardi (2012), who investigated the impacts of round gobies on benthic communities through field surveys. They found that macroinvertebrate diversity and dominance by large-bodied taxa declined with increasing goby density, and that benthic algal biomass increased with goby density across sites, suggesting a trophic cascade driven by goby predation on benthic grazers. Therefore, it seems that the ability of round gobies to elicit trophic cascades through top-down effects varies significantly in time and space, even within the same system. This presents a whole new level of context-dependence, previously highlighted by variability of an invader's impacts across systems. Our study illustrates that the impacts of the round goby

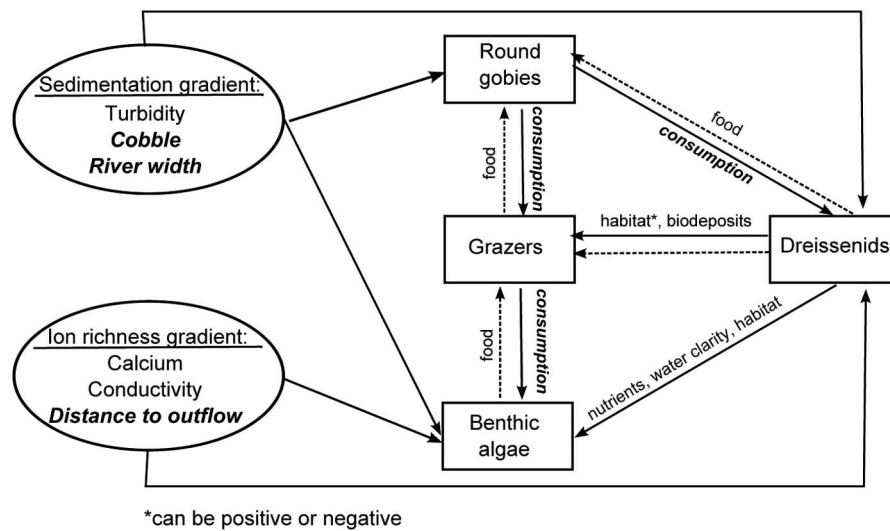


Fig. 3. Concept map of the various interactions between biotic (rectangle) and abiotic (oval) components in the food web investigated in this study. All arrows lead from the causal variable to the response variable. Interactions between biotic components under bottom-up control (dashed arrows) and top-down control (solid arrows) are included, as well as a brief description of mechanism for the interaction. Negative interactions are indicated with bold arrows and bold, italicized font; positive interactions are indicated by normal arrows and font. The asterisk on “habitat” for interaction between dreissenids and grazers signifies that this interaction can have both positive and negative effects on the grazers, depending on the size of the organism. Large grazers may be excluded from mussel-covered substrate (Ricciardi et al. 1997), whereas the interstitial spaces between dreissenid shells are used by small invertebrates for refugia from predation.

varies significantly over time and space within the same system. The next step will be to determine whether this impact variation results from factors such as: (1) spatiotemporal variation in nutrient inputs; (2) annual variation in water temperature; (3) changes to river volume; and (4) round goby population structure, including size distribution. The St. Lawrence River receives a significant inflow of nutrients from neighboring municipalities and from agricultural activity in the watershed (Hudon and Bibeault 2006), and has experienced extreme temporal variability in water levels (Hudon and Bibeault 2006). Climate change is also having effects on the St. Lawrence River, where the annual temperature is on the rise, and the lowering mean water level of the Great Lakes is expected to lead to a significant loss of outflows from Lake Ontario into the St. Lawrence River (Crowley 2003). Lower water levels as well as higher water temperatures could lead to chronic nutrient enrichment and higher productivity in the St. Lawrence River, leading to dominance of bottom-up effects. On the other

hand, round gobies are relatively new to the St. Lawrence River, and tend to be smaller than those in longer established populations in the Great Lakes (Kipp and Ricciardi 2012). Over time, we could see a shift in the round goby population structure in the river towards larger individuals, leading to stronger top-down effects.

In summary, we found that the interaction between round gobies and benthic communities are strong, and patterns in benthic community abundance and diversity better reflect these interactions than a suite of abiotic variables. However, in our study, the directionality of these interactions differed from those found in a previous study investigating the same organisms in the same system. Therefore, while the interactions between round gobies and benthic communities remain strong, the direction of these interactions varies over space and time. Determining factors that trigger the switch between top-down and bottom-up control is essential to predicting the ecological impacts of round goby invasion.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A and B are available online: <http://dx.doi.org/10.1890/ES15-00371.1.sm>