

# Serial introductions modify a trophic cascade and partially mitigate changes in lake ecosystem structure

David C. Richardson<sup>1,2</sup>, Emma C. Bruno<sup>1,3</sup>, Hailee L. Edwards<sup>1,4</sup>, Dejea M. Green<sup>1,5</sup>,  
Anthony J. Hollander<sup>1,6</sup>, Sawyer R. McFadden<sup>1,7</sup>, Kayla A. Reid<sup>1,8</sup>, and Heather L. Wander<sup>1,9</sup>

<sup>1</sup>Biology Department, SUNY New Paltz, 1 Hawk Drive, New Paltz, New York 12561 USA

**Abstract:** New species introductions can change lakes rapidly by directly affecting trophic levels through predator–prey interactions or by indirectly affecting ecosystem structure and function. When successive (serial) introductions occur with time between the introductions for each population to become established, there could be permanent shifts in the ecosystem or a return to a prior state if 1 or more introduced species is removed. We used a natural experiment where, in a fishless lake with a simple pelagic zooplankton–phytoplankton food web, the introduction of a zooplanktivorous fish species was followed by the introduction of a piscivorous fish species. Following the loss of the introduced zooplanktivore, the piscivore population shifted from a growing unimodal population dominated by small individuals to a shrinking bimodal population. Zooplankton density remained relatively constant, but zooplankton size increased and composition shifted towards larger-bodied taxa. Phytoplankton biomass decreased, which allowed water clarity to increase and return to pre-fish introduction levels. We used our results to make predictions about the importance of serial introductions in controlling lake food webs and ecosystem structure. Some introductions lead to trophic cascades that broadly affect lake ecosystems but, following serial introductions of a higher-trophic level, ecosystem structure and function could potentially recover.

**Key words:** fish introductions, trophic cascade, serial introductions, piscivore, zooplanktivore, lake ecosystem

Introduced fish species that occupy upper trophic levels can directly affect the trophic levels above and below them through predator–prey interactions (Carpenter et al. 2011) or indirectly affect the foodweb and ecosystem structure and function via top-down control (Richardson et al. 2016). Visual predation by introduced zooplanktivorous fish alters plankton communities by eliminating or reducing large pelagic zooplankton (Brooks and Dodson 1965). This consumption of large zooplankton can result in a trophic cascade that releases the primary producers from top-down control and yields increased primary producer biomass and decreased water clarity (Flecker and Townsend 1994, Simon and Townsend 2003, Baxter et al. 2004, Ellis et al. 2011, Richardson et al. 2016).

The success of an introduced species in a new environment is often enhanced by freedom from predation, parasites, or pathogens in the new ecosystem (i.e., enemy release hypothesis, Colautti et al. 2004). For example, an introduced zooplanktivorous fish species could represent the

upper trophic level in a fishless lake and, in the absence of piscivores, possibly experience rapid population growth that initiates a trophic cascade (Brooks and Dodson 1965, Richardson et al. 2016). Trophic cascades mediated by introduced fish can result in ecosystem regime shifts that are permanent while the introduced species remains in the new environment (Zavaleta et al. 2001, Folke et al. 2004). For example, the introduction of a fish species can cause an entire aquatic ecosystem to shift states from clear to turbid and change the interactions between the species that inhabit the ecosystem (Holling 1973, Levin and Lubchenco 2008, Carpenter et al. 2011). Introduced species populations could instead experience a sudden collapse, with the possibility of local extinction, in isolated lakes with little connectivity to other populations (Simberloff and Gibbons 2004). Foodweb and ecosystem structure may return to a prior state if the introduced species is removed via predation, competition, or human directed management (Elser et al. 2000, Lepak et al. 2006, Daskalov et al. 2007, Sønder-

E-mail addresses: <sup>2</sup>richardsond@newpaltz.edu; <sup>3</sup>brunoe2@hawkmil.newpaltz.edu; <sup>4</sup>edwards\_hailee@yahoo.com; <sup>5</sup>greend6@hawkmil.newpaltz.edu; <sup>6</sup>hollanda2@hawkmil.newpaltz.edu; <sup>7</sup>mcfaddes1@hawkmil.newpaltz.edu; <sup>8</sup>reidk2@hawkmil.newpaltz.edu; <sup>9</sup>wanderh1@hawkmil.newpaltz.edu

gaard et al. 2017). However, ecosystems with introduced species that have collapsed could instead be left with residual impacts (Simberloff and Gibbons 2004).

Serial introductions of species are 2 successive introductions of different species that occur with enough time between the introductions for the population of the 1<sup>st</sup> introduced species to become established. Serial introductions could result in the collapse of 1 or more of the introduced species if the 2 taxa are predators and prey. For example, in a fishless lake with a simple pelagic zooplankton–phytoplankton food web, the introduction of a zooplanktivorous fish species was followed by a piscivorous fish species introduction several years later (Charifson et al. 2015). The 1<sup>st</sup> fish introduction resulted in a trophic cascade that caused the lake to have higher productivity than before the zooplanktivorous fish was introduced (Richardson et al. 2016). However, the subsequent introduction of a piscivore resulted in the complete collapse and extirpation of the zooplanktivores. Aquatic invaders cause the largest indirect and nonlinear effects on other components of the ecosystem by building new ecosystem links (Simon and Townsend 2003). Therefore, serial introductions could facilitate a rapid return of ecosystem structure to pre-introduction states, especially if the 2<sup>nd</sup> introduced species controls the 1<sup>st</sup> introduced species via predation.

We used the previous example of a formerly fishless lake with serial introduction of 2 species of fish (Charifson et al. 2015, Richardson et al. 2016) as a natural experiment in which we explored if there was return to prior ecosystem structure following the loss of an introduced zooplanktivore, despite the remaining presence of the introduced piscivore. We hypothesized that the introduction and loss of an intermediate zooplanktivorous trophic level would affect upper and lower trophic levels and ecosystem structure in the following ways: 1<sup>st</sup>, piscivorous fish, after losing their primary food source, will decrease in population size and larger fish will become dominant; 2<sup>nd</sup>, following the release from predation, zooplankton density will increase, and larger taxa will increase in prevalence; 3<sup>rd</sup>, the zooplanktivore driven trophic cascade will experience a reversal and result in decreasing algal biomass. Finally, ecosystem structure will respond to decreasing algal biomass with increased water transparency and decreasing hypolimnetic hypoxia.

## METHODS

### Study sites

Our 3 study lakes, Lake Minnewaska, Lake Awosting, and Mohonk Lake, are located on the Shawangunk Ridge, mid-Hudson Valley, New York, USA. The lakes were glacially formed and are primarily rain-fed with small watersheds and minimal groundwater exchange (Caine et al. 1991). The watershed of each lake has underlying erosion-resistant quartz conglomerate and sandstone, but Mohonk also has an inlier of Martinsburg shale within the quartz conglomerate

(Menking et al. 2012). Minnewaska is close to neutral (pH = 6.5) because of buffering by gravel hiking trails, Awosting is acidic (pH = 4.5) because of acid rain, and Mohonk is neutral (pH = 7.5) because of buffering by the shale inlier (Richardson et al. 2018). These lakes reside within protected lands and are minimally affected by local land use.

The 3 lakes have different food webs, even though they are close (~10 km) to each other. We compared Awosting, a fishless lake, and Mohonk, a lake with multiple fish trophic levels, to Minnewaska, the lake that recently experienced the serial introductions of piscivores described above. Awosting is an oligotrophic, clear-water lake with no fish observed in the previous 100 y (Smiley and Huth 1983). Mohonk is a mesotrophic lake that contains a diverse fish assemblage that includes shiners, Largemouth Bass, and various other species of sunfish, bass, and trout (Smiley and Huth 1983). Landowners who operate a lakeside hotel have stocked fish in Mohonk for recreation since 1871 (Smiley and Huth 1983).

In contrast to Awosting and Mohonk, Minnewaska has had a more dynamic history. Minnewaska had been fishless since the 1920s because of acid rain that resulted in low lake pH (Smiley and Huth 1983). However, pH in this lake increased recently (Richardson et al. 2018), and it became viable for fish survival and reproduction in ~2005. In 2008, Golden Shiners (*Notemigonus crysoleucas*, a small minnow, hereafter shiners) were unintentionally introduced to Minnewaska (Charifson et al. 2015). As a result, a trophic cascade occurred because these shiners consumed zooplankton grazers, which led to increased algal blooms and shifted the lake from oligotrophy to mesotrophy in 2011 (Richardson et al. 2016). Largemouth Bass (*Micropterus salmoides*, hereafter bass) were subsequently introduced in 2012, also unintentionally (Charifson et al. 2015). Shiners have not been found in the lake since 2014, probably as a result of bass predation (Charifson et al. 2015). The loss of shiners allows us to test our above hypotheses by comparing communities and ecosystem function over time in Minnewaska and over space between the 3 different lakes.

### Sampling overview

We took biological and chemical measurements (described below) in both pelagic (1 per lake) and littoral (4–5) sites in each lake. In Minnewaska and Awosting, the pelagic sites were located at the deepest part of the lake (Table 1), but in Mohonk the pelagic site is at the end of a wharf at 13-m depth to match an existing long-term sampling site. We sampled the pelagic and littoral sites of each lake 2 to 5× each summer (Jun–Sep) from 2013 to 2016. At each of these times we sampled all 3 lakes within a 2-d period, and used the samples for cross-lake comparisons. We also sampled water transparency and phytoplankton biomass

Table 1. Characteristics of the 3 study lakes. The fish column indicates presence or absence of fish.

Lake name	Lat (°N)	Long (°W)	Max depth (m)	Mean depth (m)	Surface area (ha)	Fish
Minnewaska	41.726	-74.235	23	5.7	13.8	Yes <sup>1</sup>
Awosting	41.706	-74.290	29	5.0	39.0	No
Mohonk	41.766	-74.158	19	6.0	6.9	Yes <sup>2</sup>

<sup>1</sup> Golden Shiners introduced in 2008; Largemouth Bass in 2011; only bass were present 2015–2017

<sup>2</sup> Fish stocked since 1871; fish assemblage includes Golden Shiners, various species of bass and trout (Smiley and Huth 1983)

(see below) in Minnewaska every 1 to 2 wk during the ice-free season from 2012 to 2016.

### Bass population

To test the effect of the loss of shiners on upper trophic levels in Minnewaska we used catch–mark–recapture and electrofishing methods to measure bass population size each summer from 2012 to 2016, with assistance from the New York State Department of Environmental Conservation (NYSDEC) (see Charifson et al. 2015 for methods and 2013–2014 results). Electrofishing was done 2× each summer. Population size and standard error were estimated with Peterson's method after the final recapture (Krebs 1998, Charifson et al. 2015). Bass were present in 2012, but we did not catch enough ( $n = 4$ ) for mark and recapture calculations. We compared all pairwise population sizes with  $t$ -tests, and used a Bonferroni correction to adjust  $\alpha$  for the 6 pairwise comparisons between all years (adjusted  $\alpha = 0.008$ ). We also measured fish length, from mouth to caudal fin, of each fish captured. The fish length data were not normal, so we compared mean lengths between years with a Kruskal–Wallis nonparametric analysis of variance (ANOVA) and did a post-hoc Dunn test for means comparisons (R package *dunn.test*, Dinno 2017).

### Zooplankton

To test the loss of zooplanktivorous shiners and predation on lower trophic levels, we collected zooplankton with 10-m tows with an 80- $\mu$ m Wisconsin Plankton Net (Wildco, Yulee, Florida) over 4 consecutive y (2013–2016) at all 3 lakes. We counted between 35 and 100 individuals (ind) per sample, measured their length with an ocular micrometer, and identified them to order or suborder based on an online zooplankton key (Haney et al. 2013). We calculated volumetric density and mean body length during each sampling event. Calanoida and Cladocera, the 2 focal taxa for this study, represent small-bodied and large-bodied zooplankton orders or suborders whose relative abundances

indicate size-selective predation (Brooks and Dodson 1965, Werner and Hall 1974). We calculated percent Calanoida and Cladocera based on the total number of zooplankton collected in each sample. For each lake we used Thiel-Sen's Slopes to estimate trends in interannual zooplankton density, size, % Calanoida, and % Cladocera (R package *mblm*; Komsta 2013).

### Phytoplankton biomass

To test the loss of shiners and potential cascading effects on the base of the food web, we used chlorophyll *a* (Chl *a*) concentration as a proxy to examine temporal trends in phytoplankton biomass at pelagic and littoral sites. We included only data from when the lakes were stratified (01 Jun–15 Oct) from 2012 to 2016. We do not have pelagic data for Awosting, or from any Mohonk site from 2012. We used a hot ethanol extraction and spectrophotometry to measure Chl *a* concentration (Richardson et al. 2009). We assessed interannual trends for the pelagic and littoral sites in each lake by calculating the Thiel-Sen's slope of Chl *a* concentrations.

### Water clarity

To test if the loss of shiners affected temporal trends of water clarity, Secchi depth measurements were compiled for Minnewaska and Mohonk pelagic sites from 3 different sources: Mohonk Preserve, New York State Environmental Management Bureau (EMB), and sampling from this study. Mohonk Preserve staff and volunteers collected weekly measurements between 1995 and 2016 at the pelagic site in Mohonk. EMB collected from 1 to 15 measurements per year between 1995 and 2016 at the pelagic site in Minnewaska. We collected Secchi depths weekly to biweekly at the pelagic site in Minnewaska from 2013–2016. Data was not available for Awosting. To make the comparisons across lakes and datasets consistent, we only analyzed data from Jun to Aug, when collection frequency was highest for both Mohonk and Minnewaska. We partitioned all Secchi depth data into 3 time periods based on the presence or absence of shiners in Minnewaska as follows: 1) prior to shiner arrival (1995–2007: 'pre'), 2) during shiner presence (2008–2013: 'during'), and 3) following the loss of shiners (2014–2016: 'post'). The 'Pre' and 'During' data for both lakes are published in Richardson et al. (2016). For each lake, we used Kruskal–Wallis nonparametric ANOVAs to compare the 3 time periods, and used Dunn's post hoc test for pairwise comparisons among time periods (Dinno 2017). To verify that phytoplankton biomass was related to water clarity in Minnewaska, we did a linear regression between Chl *a* concentration and Secchi depth during the ice-free period. We natural log transformed both variables to satisfy linear regression assumptions of bivariate normal distributions.

### Hypolimnetic hypoxia

To test the indirect effects of the loss of shiners on lake dissolved oxygen (DO), we measured hypoxia in the hypolimnion of Minnewaska during summer stratification. We took profiles of DO and temperature at the Minnewaska pelagic site with a luminescent DO sensor (LDO101 Rugged LDO Probe; Hach, Loveland, Colorado) every 1 to 2 wk between 1 Jun and 15 Oct each year (2012–2016). We identified the depth of hypoxia as the 1<sup>st</sup> sampling depth from the surface at which DO concentrations were <2 mg/L. We calculated the % of lake volume that was hypoxic by multiplying the depth of hypoxia by the known percentage of volume of the lake at that depth based on bathymetry data. We determined the rate of increase of hypoxic lake extent each year by fitting a linear regression model to the relationship between the day of the year and % lake volume hypoxia. To examine possible drivers of hypoxia in Minnewaska, we calculated the linear trends of annual Chl *a* concentrations during the pre-stratification (21 Mar–21 Jun) and stratified (1 Jun–15 Oct) periods at both pelagic and littoral sites. To determine if primary producer biomass could explain summer hypoxia dynamics, we compared residuals from the linear analysis to annual maximum hypoxic volume and the rate of hypoxic volume increase. The data were not normally distributed, so we used hierarchical agglomerative cluster analysis to determine whether Chl *a* residuals followed the same patterns as hypoxia variables with groupings based on dendrograms.

## RESULTS

### Bass

We collected and marked 40 to 100 bass each year except 2012. Bass population size increased by 59% immediately after the loss of the shiners (Fig. 1A). In the following years, bass population size decreased by ~50% annually (Fig. 1A). However, the population sizes did not differ significantly between any years (all pairwise  $p > 0.008$ ). In contrast, bass length varied across all years ( $\chi^2 = 158$ ,  $df = 4$ ,  $p < 0.001$ ). Following the loss of shiners between 2013 and 2014, bass length increased significantly, by 62% (post-hoc Dunn test,  $p < 0.001$ , Fig. 1B). In 2015 and 2016, average length continued to increase significantly, but more slowly (30 [ $p < 0.001$ ] and 17% [ $p = 0.03$ ] annual increases; Fig. 1B). As bass average length increased, the distribution became increasingly bimodal with distinct groups of younger, small (~100 mm) and older, large bass (~240 mm; Fig. 1B).

### Zooplankton

Zooplankton density did not change significantly over the 4 y in any of the lakes (Fig. 2A–C;  $p > 0.05$ ). Across all years, mean zooplankton density was 11, 24, and 35 ind/L in Minnewaska, Awosting, and Mohonk, respectively. Zooplankton from Minnewaska and Mohonk (means = 0.54

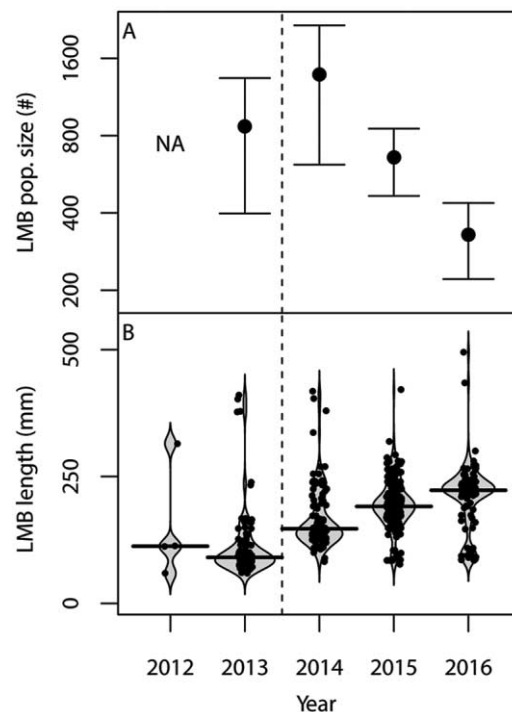


Figure 1. A.—Largemouth Bass (LMB), *Micropterus salmoides* fish population size in Minnewaska ( $\pm 1$  SE); note the  $\log_2$  scale on the y-axis. Too few fish were captured in 2012 to estimate the population size. B.—LMB individual tip-to-tail length beanplots with estimated density distributions and points for each captured fish. Annual medians are indicated with bold horizontal lines. The dashed vertical line represents the transition from shiner presence to the loss of shiners in Minnewaska.

and 0.48 mm, respectively) were larger than zooplankton from Awosting (mean = 0.32 mm). Out of the 3 lakes, average zooplankton size remained constant only in Mohonk at 0.48 mm (Fig. 2C;  $p > 0.05$ ). In Awosting the average zooplankton size decreased significantly from 2013 to 2016 (Fig. 2B;  $p < 0.001$ , rate of decrease =  $-0.05$  mm/y). In contrast, the average zooplankton size in Minnewaska increased significantly ( $p < 0.001$ ), doubling from 2013 (mean = 0.33 mm) to 2016 (mean = 0.76 mm) at a rate of 0.09 mm/y (Fig. 2A).

Over the course of our study, zooplankton assemblage composition changed more in Minnewaska than in the other 2 lakes (Fig. 3A–C). In Mohonk, % Cladocera did not increase over time ( $p = 0.16$ ). We only had 2 y of Calanoida data and did not calculate a trend because we lacked sufficient data. Over the last 2 y, percentages of both Calanoida and Cladocera were similar (Fig. 3C). Calanoida were 3 $\times$  more common than Cladocera in Awosting over the 4 y (Fig. 3B), and the % contribution to the assemblage did not change significantly over time for either taxa ( $p = 0.24$  and 0.17, respectively). Conversely, Cladocera in Minnewaska were 3 $\times$  more prevalent than Calanoida over the



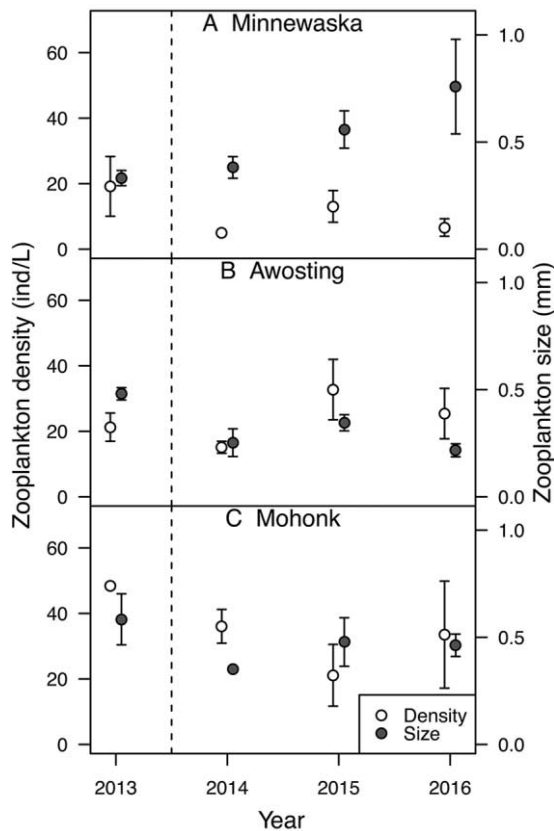


Figure 2. Mean zooplankton density (open circles) and mean size (gray circles) ( $\pm 1$  SE) compared across years of study for Minnewaska (serial introductions of fish) (A), Awosting (no fish) (B), and Mohonk (fish assemblage) (C) lakes. The dashed vertical line represents the transition from shiner presence to the loss of shiners in Minnewaska. There was only 1 sample for Mohonk size in 2014, so no error bars are presented. For all other points, error is too small to be shown.

4 y. Cladocera % increased significantly over time at 9%/y ( $p = 0.025$ ), whereas Calanoida % decreased significantly over time at 4%/y ( $p = 0.024$ ). These opposing trends resulted in Cladocera being 11 $\times$  more common than Calanoida in 2016, dominating Minnewaska zooplankton (70% of total individuals) compared to 2014 when Cladocera was only 2 $\times$  more common than Calanoida (Fig. 3A).

### Phytoplankton Biomass

Phytoplankton biomass decreased every year at all sampling sites in Minnewaska, but trends varied among the pelagic and littoral sites in both Awosting and Mohonk (Fig. 4A–C). In Minnewaska, Chl *a* concentration decreased at both littoral ( $-0.29 \mu\text{g L}^{-1} \text{y}^{-1}$ ,  $p < 0.001$ ; Fig. 4A), and pelagic sites ( $-0.26 \mu\text{g L}^{-1} \text{y}^{-1}$ ,  $p < 0.001$ ; Fig. 4A). In Awosting, Chl *a* concentrations did not change significantly at littoral sites ( $p = 0.69$ ), but decreased at the pelagic site ( $-0.14 \mu\text{g L}^{-1} \text{y}^{-1}$ ,  $p = 0.04$ ; Fig. 4B). Conversely, Chl *a* concentrations in Mohonk decreased at littoral sites

( $-0.52 \mu\text{g L}^{-1} \text{y}^{-1}$ ,  $p < 0.001$ , Fig. 4C), but did not change significantly at the pelagic site ( $p = 0.41$ ).

### Water clarity

In Minnewaska, water clarity varied significantly among the 3 time periods ( $\chi^2 = 41$ ,  $df = 2$ ,  $p < 0.001$ ). Secchi depth decreased by 57% after shiners were introduced to Minnewaska ( $p < 0.001$ ) and returned to pre-shiner values ( $p < 0.001$ , Fig. 5A) following shiner extirpation. In contrast, the Mohonk Secchi depth remained constant throughout the sampling duration ( $\chi^2 = 3.6$ ,  $df = 2$ ,  $p = 0.16$ ; Fig. 5B). In Minnewaska, Secchi depth was inversely

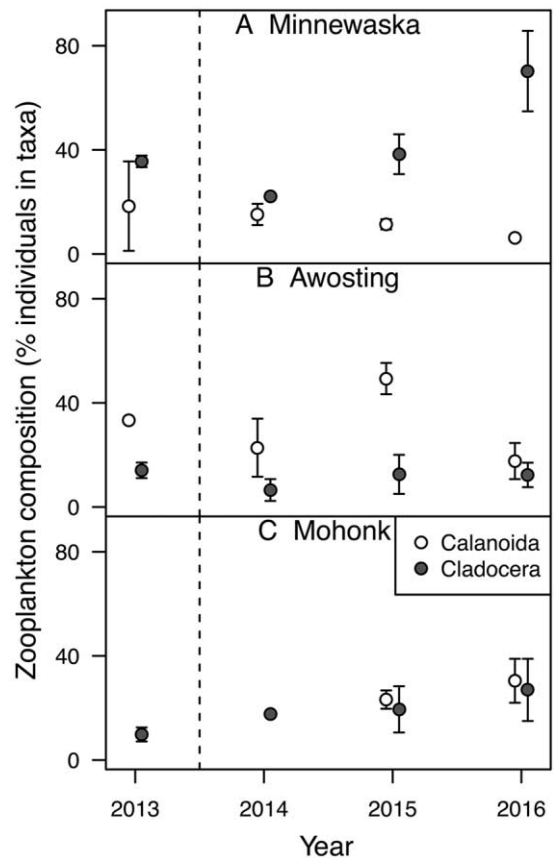


Figure 3. Mean zooplankton composition for focal taxa, Calanoida (open circles) and Cladocera (gray circles) ( $\pm 1$  SE), for Minnewaska (serial introductions of fish) (A), Awosting (no fish) (B), and Mohonk (fish assemblage) (C) lakes. The 2 numbers do not add to 100% as other taxa were collected but are not presented here. The dashed vertical line represents the transition from shiner presence to the loss of shiners in Minnewaska. Zooplankton were only identified to Subclass Copepoda in Mohonk in 2013 and 2014, so no points were included for Calanoida in those years. Points for Calanoida in Minnewaska 2016 and Awosting 2013 and for Cladocera in Mohonk 2014 show no error bars because we only had 1 sample for those lakes in those years. For all other points, error is too small to be shown.

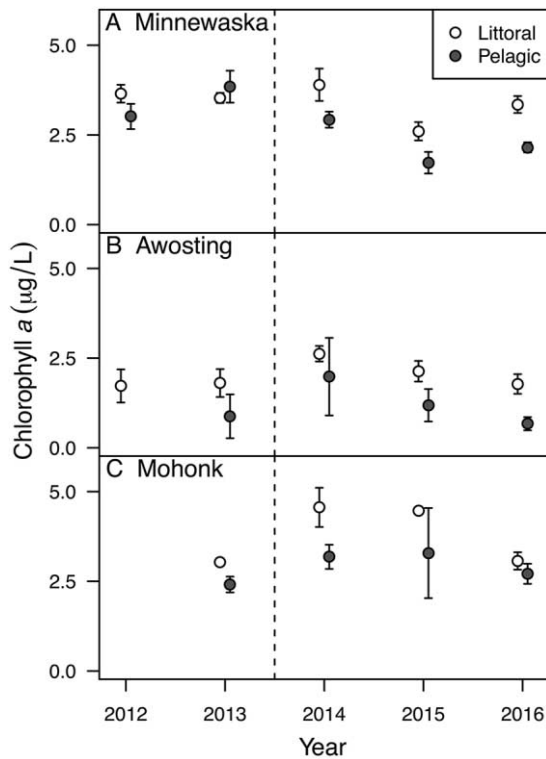


Figure 4. Mean chlorophyll *a* (Chl *a*) concentrations at littoral sites (open circles) and pelagic site (gray circles) ( $\pm 1$  SE) across years for Minnewaska (serial introductions of fish) (A), Awosting (no fish) (B), and Mohonk (fish assemblage) (C) lakes for 1 Jun to 15 Oct each year. No data were collected for Awosting and Mohonk pelagic sites and Mohonk littoral sites in 2012. Error may be too small to be shown.

and non-linearly related to phytoplankton biomass ( $\text{Secchi} = 6.3 \times \text{Chl}^{-0.44}$ ,  $R^2 = 0.30$ ,  $F_{1,43} = 19.8$ ,  $p < 0.001$ , Fig. 6).

### Hypoxia

In Minnewaska, hypoxia in the hypolimnion varied between rapid and slow onset in alternating years (Fig. 7). Hypoxic lake volume increased significantly throughout each stratified season in 2012, 2014, 2015, and 2016. The rate of increase was higher in 2012, 2014, and 2016 than in 2013 and 2015. Further, maximum hypoxic volume was  $>20\%$  of the lake in 2012, 2014, and 2016, but  $<10\%$  of the lake in 2013 and 2015. At Minnewaska littoral and pelagic sites, spring Chl *a* concentrations showed large oscillations around an interannual trend, similar to summer Chl *a* concentrations (Fig. 4A). For each year, the residuals from oscillations around the trend line grouped into above- and below-expected concentrations. When spring pelagic Chl *a* residuals were positive, maximum hypoxia was  $>20\%$  (cluster analysis, Fig. 8A) and the rate of hypoxia increase was greater than  $0.15\%/d$  (cluster analysis, Fig. 8B). Summer pelagic Chl *a* residuals similarly clustered with maximum hypoxia and rate of hypoxia increase, but had more variability than the spring pelagic residuals.

### DISCUSSION

We found that the loss of an introduced zooplanktivorous fish in Minnewaska resulted in the recovery of lake transparency via an alteration of the trophic cascade, despite the continued presence of an introduced piscivore. Following the loss of the zooplanktivores, the trophic cascade did not affect zooplankton density but it did affect zooplankton size and composition, which ultimately resulted in increased zooplankton herbivory and decreased phytoplankton biomass. Furthermore, the loss of the zooplanktivore trophic level affected the piscivore population size and structure as a result of the loss of their primary food source. Lake hypolimnetic hypoxia did not return to fishless oligotrophic conditions during this study, indicating that additional factors control deep-water oxygen concentrations.

Following the shiner extirpation and loss of the only non-conspecific fish prey, the bass population distribution appeared to shift from a growing unimodal population dominated by small individuals to a shrinking bimodal population with a range of fish sizes (Fig. 1). The population size shift may be a result of the lack of food sources available to the bass. Bass begin their life feeding on invertebrates, and progress from consuming zooplankton to consuming

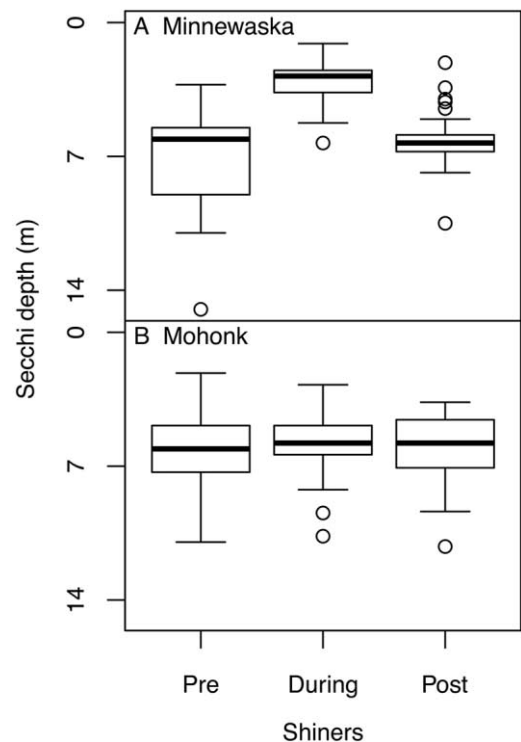


Figure 5. Secchi depth prior to the arrival of shiners (Golden Shiner, *Notemigonus crysoleucas*) (Pre, 1995–2007), during shiner presence (During, 2008–2013), and following the loss of shiners (Post, 2014–2016) in Lake Minnewaska (A) and Mohonk Lake (B) Secchi depth. The bold horizontal line is the median; the box ends show the interquartile range (IQR), and the whiskers represent the  $\text{IQR} \pm 1.5 \times \text{IQR}$ .

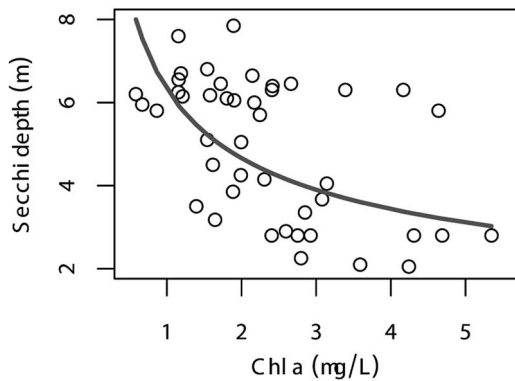


Figure 6. Secchi depth plotted against chlorophyll *a* (Chl *a*) concentrations at the Lake Minnewaska pelagic site from 1 Jun to 15 Oct, 2012 to 2016. The best-fit power function model is shown in gray (Secchi =  $6.3 \times \text{Chl}^{-0.44}$ ).

benthic insect larvae (Olson 1996). Bass then, while they are <1 y old, experience an ontogenetic diet shift when they become large enough to feed on small fish in addition to macroinvertebrates (Christensen and Moore 2009). However, bass >300 mm in length feed on fish almost exclusively (Christensen and Moore 2009). Shiners are an ideal food source for bass, and bass presence in a lake can directly control shiner populations if bass have no other resources (Mittelbach et al. 1995). Bass population size increased from 2013 to 2014, probably because of the abundant prey and lack of interspecific competition (Fig. 1). Following the elimination of the shinners, bass probably shifted to intraspecific predation (Post et al. 1998) since there were no other fish prey species. Both adult and juvenile bass can exhibit high amounts of cannibalism, reaching up to 70% for a stable population (DeAngelis et al. 1980, Post 2003). Therefore, the medium-sized bass (200–250 mm) will probably prey on fingerlings and small bass in Minnewaska, leading to the bimodal distribution observed in this study (Fig. 1).

By 2016, bass size appeared to follow a bimodal distribution with a gap in the 75- to 200-mm range (Fig. 1B), the size that corresponds to 1- and 2-y-old bass (Ludsin and DeVries 1997, Charifson et al. 2015). Presumably, this cohort was most heavily affected by cannibalism by the largest bass following the loss of the shinners (DeAngelis et al. 1980, Post et al. 1998). We hypothesize that there are 2 possible future outcomes for this bass population: stable cycles or a population crash and extirpation. The bass population may stabilize in a cyclical pattern that alternates between a small population dominated by large bass that have high predation and reproductive rates, and a large population dominated by smaller bass that have lower survival and reproductive rates (Persson et al. 2003). The few small bass that survive will ultimately replace the larger bass. Instead, the bass population could crash, causing the lake to return to a fishless state if the predation rates of the few large bass

are too high (Simberloff and Gibbons 2004) or if there is a particularly long winter and there are anoxic conditions under ice when the population is small (e.g., Mittelbach et al. 1995).

The population size of large-bodied zooplankton (e.g., Cladocera) generally decline more than other zooplankton groups when planktivorous fish are present because of size-selective predation (Brooks and Dodson 1965, Drenner et al. 1978). Large zooplankton are more conspicuous and less able to evade visual predators than some other smaller-bodied taxa (Sommer and Stibor 2002). Behavioral adaptations, such as diel vertical migration, have evolved as predator-avoidance tactics (Gliwicz 1986, Lampert 1989, Farrell and Hodgson 2012), but might not be present in the Minnewaska zooplankton assemblage because of the 90-y history without fish (Charifson et al. 2015). Thus, the large-bodied zooplankton in Minnewaska were probably more

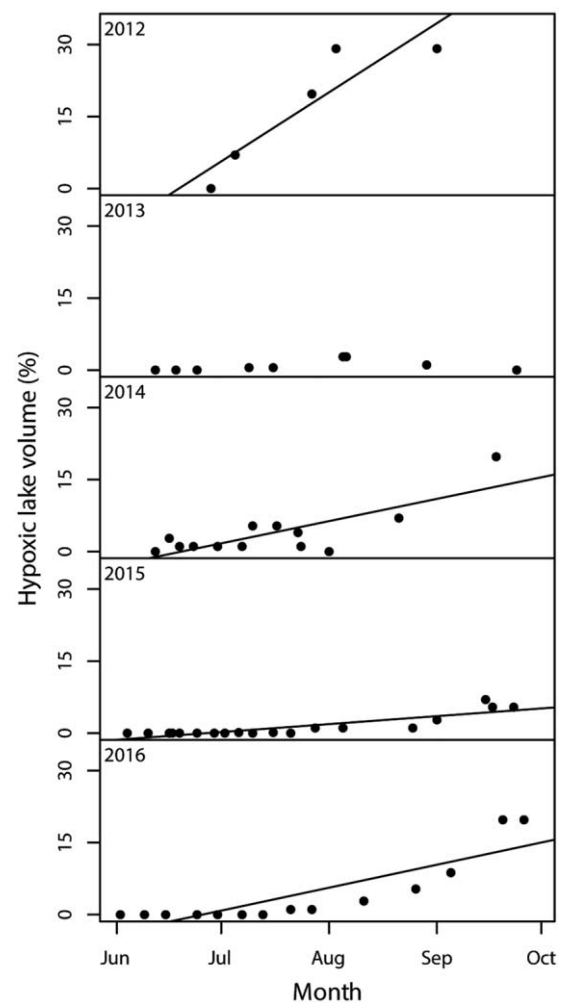


Figure 7. The % of Lake Minnewaska volume that is hypoxic (<2 mg/L, black circles) from 2012 to 2016. Significant linear regression lines between hypoxic lake volume and day of year are displayed.

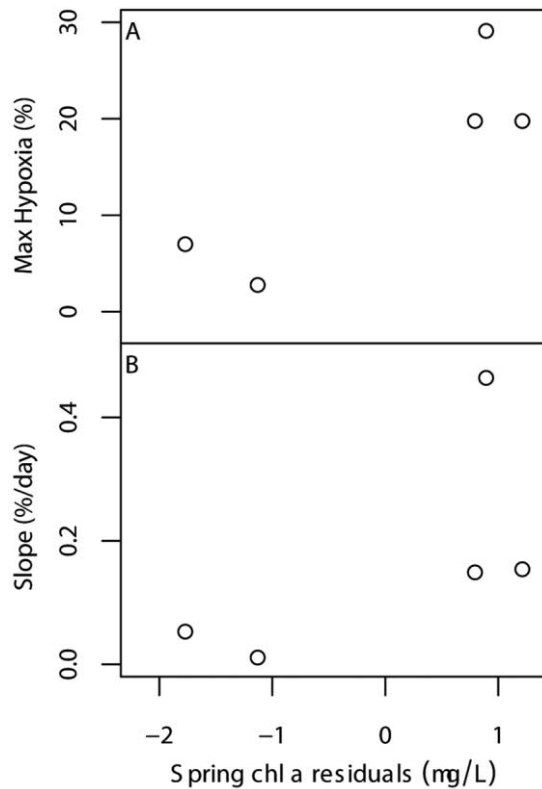


Figure 8. A.—maximum hypoxic lake volume (%) measured each year. B.—rate of change in hypoxic lake volume (%/d) compared to detrended mean chlorophyll a (Chl *a*) concentrations from Minnewaska littoral sites each spring (21 Mar–21 Jun, 2013–2016).

susceptible to predation than small-bodied zooplankton after the introduction of zooplanktivorous shiners. After the loss of the shiners in Minnewaska, zooplankton density did not change but mean zooplankton size increased (Fig. 2A), indicating a release of large-bodied zooplankton from predation pressure and competitive exclusion of small individuals by large zooplankton.

Zooplankton assemblage composition is often structured by both taxa-specific predation and interspecific competition. During pre-shiner conditions in Minnewaska, zooplankton composition was probably similar to the current Awosting composition, where Calanoida, an order of copepods, dominates the assemblage relative to Cladocera in acidic, low cation conditions (Fig. 3A, B). Following the loss of obligate zooplanktivores in Minnewaska, Cladocera became proportionally more abundant than Calanoida, reflecting that large-bodied Cladocera are able to outcompete other taxa once they are released from predation (Brooks and Dodson 1965). Cladocera have higher feeding rates and are more mobile than rotifers and copepods, so they are more efficient grazers (Wu and Culver 1991, Agasild and Nõges 2005). The interactions between the 2 taxa may also depend on the phytoplankton composition (Burns and Schal-

enberg 2001, Sommer and Stibor 2002, Tillmanns et al. 2008). Cladocera can act as keystone predators that diversify the phytoplankton assemblage (Sarnelle 2005) and lead to decreased phytoplankton biomass, facilitating top-down control of the base trophic level in the food web (Gulati et al. 1982).

Top-down control of phytoplankton through zooplankton predation can affect the basal biomass within an ecosystem through herbivory or nutrient recycling. When predator abundance or feeding activity decreases, phytoplankton are freed from predation and, therefore, produce more biomass (Benndorf et al. 2002). In Minnewaska, within 3 y of the addition of shiners, phytoplankton biomass had increased markedly with expansive blooms of a green algae, *Spondylosium* spp. (Richardson et al. 2016). This change probably occurred because shiners freed phytoplankton from growth limits that resulted from zooplankton grazing (Pace et al. 1999). Additionally, the shiners probably cycled nutrients rapidly in the pelagic zone, promoting algal growth (Vanni and Layne 1997, Attayde and Hansson 2001). Bass also move and recycle nutrients throughout the lake (Vanni and Layne 1997) but the bass population is smaller than the peak shiner population (~15,000 individuals; Charifson et al. 2015). Since shiners have higher relative rates of nutrient cycling compared to bass (Sereda et al. 2008), fish-driven nutrient cycling has probably decreased in Minnewaska. Thus, the zooplankton assemblage probably now dominates nutrient recycling in the pelagic zone (Schindler et al. 1993).

Following the loss of shiners, phytoplankton biomass decreased by  $\sim 0.3 \mu\text{g Chl } a \text{ L}^{-1} \text{ y}^{-1}$  at both pelagic and littoral sites (Fig. 4A) presumably as a result of increased zooplankton feeding and decreased nutrient availability. Small bass are generalists that feed on benthic invertebrates but can still consume zooplankton. Thus, bass predation on zooplankton might limit increasing zooplankton densities and prevent top-down control on phytoplankton biomass preventing a return to pre-shiner levels (Post et al. 1998, García-Berthou 2002). Interannual variability in phytoplankton biomass can be controlled by a trophic cascade that varies in strength and is triggered by upper trophic level predators (Jassby et al. 1990). Therefore, if the Minnewaska bass populations cycle, phytoplankton biomass trends could follow. In years where large piscivorous bass dominate, phytoplankton biomass may decrease, whereas in years with high levels of bass reproduction the smaller zooplanktivorous bass could fill the role of the shiners, allowing increased phytoplankton growth.

Changes to foodweb structure and phytoplankton biomass can result in state shifts from oligotrophic towards eutrophic conditions and may ultimately affect water clarity (Carpenter and Cottingham 1997). In Mohonk, water clarity did not change between 1995 and 2016 (Fig. 5B) indicating that regional factors such as climate were not critical



drivers of lakes in this area, including Minnewaska. Minnewaska has minimal shoreline erosion and few inflowing tributaries, so sediment loading probably does not affect lake clarity. Minnewaska has been recovering from acidification (Richardson et al. 2018) and dissolved organic carbon (DOC) has probably increased with subsequent decreasing water clarity (Williamson et al. 2015). This may have exacerbated the declines in water clarity seen during shiner presence (Fig. 5A). However, water clarity is correlated with Chl *a* in Minnewaska (Fig. 6), indicating phytoplankton biomass has a substantial role in regulating transparency. With the loss of shiners, the trophic cascade was modified and lake transparency returned to pre-shiner Secchi depths.

Our original hypothesis was that hypolimnetic oxygen consumption would decrease after phytoplankton production decreased and water clarity in the pelagic zone increased (e.g., Carrick et al. 2005). However, hypoxia alternated between high and low maximum volumes every other year (Fig. 7) rather than steadily decreasing as the trophic state of the lake shifted from mesotrophic to oligotrophic conditions. These oscillations suggest that annual primary production is not the sole driver of hypoxia. Instead, hypoxia varied interannually with the residuals of spring phytoplankton biomass (Fig. 8A) and may be more closely linked with interannual variability in weather. For example, a heat wave caused severe hypolimnetic oxygen depletion in 2 European lakes that only lasted for a single year (Janowski et al. 2006). Mild winters, early springs, and warm summers can cause years with greater hypolimnetic hypoxia because warmer air temperatures lead to stronger and earlier stratification (Rempfer et al. 2010, Butcher et al. 2015, Kraemer et al. 2015). This climatic trend may also allow phytoplankton blooms to occur earlier and further increase the amount of summer hypolimnetic hypoxia (Gerten and Adrian 2000, Mallin et al. 2006). The timing of precipitation each season may also drive phytoplankton blooms and facilitate difference duration and magnitude of hypoxia within the lake (Paerl et al. 1998).

The strong trophic cascade that resulted from shiners may continue to affect the lake ecosystem and food web for many years, even though they are no longer present. When shiners were present before the bass introduction, primary production was elevated and resulted in substantial decreases in water clarity (Fig. 5A, B; Richardson et al. 2016). Dead phytoplankton accumulate as sediment biomass from productivity throughout the year (Defore et al. 2016, Biddanda et al. 2018), especially when decomposition rates are low because of anoxia in sediments (Killgore and Hoover 2001). Sediment-associated P that is released under hypoxic conditions could control phytoplankton biomass through internal loading during lake turnover events (Vrede et al. 2009). Thus, the legacy of organic matter in the sediment generated during high productivity years may persist even though annual production of phytoplankton biomass has decreased since the loss of the shiners (Fig. 4A–C).

### Proposed hypotheses for the consequences of serial introductions

We can use this study to generate hypotheses about serial introductions. The largest impacts from introduced species occur when new species create links between different components of the food web or result in trophic cascades (Simon and Townsend 2003, Carlsson et al. 2004, Ricciardi et al. 2013). Therefore, we hypothesize that serial introductions will increase ecosystem resiliency to community and ecosystem-level effects if the introductions occur in adjacent, upper trophic levels with minimal top-down control and low biotic resistance. Introduced species can compete with organisms with similar diets that already occupy that trophic level, and may even exacerbate the magnitude of the trophic cascade through exploitation of resources (e.g., Arismendi et al. 2012). However, introductions in adjacent trophic levels may affect a previously introduced species via top-down or bottom-up controls on predation. Here, shiners experienced a release from predation when they invaded a formerly fishless lake, which allowed rapid population growth (Charifson et al. 2015). We propose a corollary to the enemy release hypothesis (Colautti et al. 2004)—that a successive introduction in the adjacent, upper trophic level will enhance predatory control of the initial introduced species. The effects from a trophic cascade are greatest when higher predators are lacking (Casini et al. 2009), so food webs are most susceptible to this type of effect in isolated habitats like lakes and oceanic islands that cannot support high-level predators (Pimm 1987). In this study, the upper trophic levels were absent because of the history of acid rain (Richardson et al. 2018). Finally, biotic resistance, through a diverse community, is more likely to limit establishment, population growth, and wide-spread impacts of large predators (Ricciardi et al. 2013). Biotic resistance here was low because of the lack of fish and little-or-no functional redundancy with tertiary (zooplanktivore) and quaternary (piscivore) consumers. This allowed both the success of the 1<sup>st</sup> introduced species and the rapid return of foodweb and ecosystem level effects following the 2<sup>nd</sup> introduction (e.g., Fig. 5A).

### Conclusions

Serial introductions are occurring in freshwater systems around the world (Ruesink 2005, Gozlan et al. 2010). For example, the Great Lakes ecosystem and ecological communities have experienced >180 introductions from shipping, stocking, and other human activities, but there has been difficulty in establishing the cumulative or synergistic effects of serial introductions (Vander Zanden et al. 2010, Pagnucco et al. 2015). Our study provides an example of serial introductions and the ecosystem-wide effects resulting from each introduction. Changes to the lake indicate that removing introduced intermediate trophic levels could be an effective management strategy for reversing the unwanted effects of trophic cascades. However, we are not advocating

for additional species introductions to manage for the deleterious effects of an earlier invader given the complex circumstances under which trophic cascades occur. Removing a species via electrofishing or overfishing has been employed as a possible management strategy to restore ecosystem structure (Lepak et al. 2006, Daskalov et al. 2007, Søndergaard et al. 2017). Some trophic cascades result in permanent state shifts (Folke et al. 2004), but it is possible for an ecosystem to at least partially recover, in terms of ecosystem structure and function, after serial introductions of apex predators.

### ACKNOWLEDGEMENTS

Author contributions: all co-authors made contributions to the following 3 tasks: 1) collected field data, processed data in the lab, or both; 2) contributed to experimental design and data integration, analysis, and interpretation; 3) contributed substantially to drafting and revising the manuscript. All co-authors read and explicitly approved the final manuscript.

This research was funded by the SUNY New Paltz Summer Undergraduate Research Experience; SUNY New Paltz Provost Challenge Grant, SUNY New Paltz Collegiate Science and Technology Entry Program; SUNY New Paltz Louis Stokes Alliances for Minority Participation; NSF Division of Environmental Biology #1144627 to J. Cole, Mohonk Preserve; Loewy Family Foundation Fellowship to DCR; NYS Water Resources Research Grant to DCR, J. Thompson, and K. Weathers and NSF Division of Environmental Biology #EF-113732 to K. Weathers. We thank interns and field volunteers for sample collection and lab processing and collaborators for interactions and data collection including the New York State Office of Parks, Recreation and Historic Preservation's Environmental Management Bureau, Mohonk Preserve, and Mohonk Mountain House, especially Dr Elizabeth Long, Paul Huth, and the Smiley Family. We thank Dr Jennifer Brentrup for comments that improved earlier versions of this manuscript.

### LITERATURE CITED

- Agasild, H., and T. Nøges. 2005. Cladoceran and rotifer grazing on bacteria and phytoplankton in two shallow eutrophic lakes: in situ measurement with fluorescent microspheres. *Journal of Plankton Research* 27:1155–1174.
- Arismendi, I., J. Gonzalez, D. Soto, and B. Penaluna. 2012. Piscivory and diet overlap between two non-native fishes in southern Chilean streams. *Austral Ecology* 37:346–354.
- Attayde, J. L., and L.A. Hansson. 2001. Fish-mediated nutrient recycling and the trophic cascade in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1924–1931.
- 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.
- Benndorf, J., W. Böing, J. Koop, and I. Neubauer. 2002. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater biology* 47:2282–2295.
- Biddanda, B. A., A. D. Weinke, S. T. Kendall, L. C. Gereaux, T. M. Holcomb, M. J. Snider, D. K. Dila, S. A. Long, C. VandenBerg, and K. Knapp. 2018. Chronicles of hypoxia: time-series buoy observations reveal annually recurring seasonal basin-wide hypoxia in Muskegon Lake—A Great Lakes estuary. *Journal of Great Lakes Research* 44:219–229.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.
- Burns, C. W., and M. Schallenberg. 2001. Calanoid copepods versus cladocerans: consumer effects on protozoa in lakes of different trophic status. *Limnology and Oceanography* 46:1558–1565.
- Butcher, J. B., D. Nover, T. E. Johnson, and C. M. Clark. 2015. Sensitivity of lake thermal and mixing dynamics to climate change. *Climatic Change* 129:295–305.
- Caine, J. S., D. R. Coates, N. P. Timoffeef, and W. D. Davis. 1991. Hydrogeology of the Northern Shawangunk Mountains. New York State Geological Survey open file report no. 1g806. New York State Geological Survey, Syracuse, New York.
- Carlsson, N. O., C. Brönmark, and L.A. Hansson. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85:1575–1580.
- Carpenter, S. R., J. J. Cole, M. L. Pace, R. Batt, W. A. Brock, T. Cline, J. Coloso, J. R. Hodgson, J. F. Kitchell, and D. A. Seekell. 2011. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079–1082.
- Carpenter, S. R., and K. L. Cottingham. 1997. Resilience and restoration of lakes. *Conservation Ecology* 1:1–17.
- Carrick, H. J., J. B. Moon, and B. F. Gaylord. 2005. Phytoplankton dynamics and hypoxia in Lake Erie: a hypothesis concerning benthic–pelagic coupling in the central basin. *Journal of Great Lakes Research* 31:111–124.
- Casini, M., J. Hjelm, J. C. Molinero, J. Lövgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 106:197–202.
- Charifson, D. M., P. C. Huth, J. E. Thompson, R. K. Angyal, M. J. Flaherty, and D. C. Richardson. 2015. History of fish presence and absence following lake acidification and recovery in Lake Minnewaska, Shawangunk Ridge, NY. *Northeastern Naturalist* 22:762–781.
- Christensen, D. R., and B. C. Moore. 2009. Using stable isotopes and a multiple-source mixing model to evaluate fish dietary niches in a mesotrophic lake. *Lake and Reservoir Management* 25:167–175.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721–733.
- Daskalov, G. M., A. N. Grishin, S. Rodionov, and V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America* 104:10518–10523.
- DeAngelis, D., D. Cox, and C. Coutant. 1980. Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. *Ecological Modelling* 8:133–148.
- Defore, A. L., A. D. Weinke, M. M. Lindbäck, and B. A. Biddanda. 2016. Year-round measures of planktonic metabolism reveal net autotrophy in surface waters of a Great Lakes estuary. *Aquatic Microbial Ecology* 77:139–153.
- Dinno, A. 2017. dunn.test: Dunn's Test of multiple comparisons using rank sums. R package version 1.3.5. (Available from: <https://CRAN.R-project.org/package=dunn.test>)

- Drenner, R. W., J. R. Strickler, and W. J. O'Brien. 1978. Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. *Journal of the Fisheries Board of Canada* 35:1370–1373.
- Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray, and B. S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* 108:1070–1075.
- Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann, and R. W. Sterner. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408:578–580.
- Farrell, A. M., and J. R. Hodgson. 2012. Zooplankton diel vertical migrations in lakes of contrasting food webs. *Bios* 83:12–16.
- Flecker, A. S., and C. R. Townsend. 1994. Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications* 4:798–807.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557–581.
- García-Berthou, E. 2002. Ontogenetic diet shifts and interrupted piscivory in introduced largemouth bass (*Micropterus salmoides*). *International Review of Hydrobiology* 87:353–363.
- Gerten, D., and R. Adrian. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnology and Oceanography* 45:1058–1066.
- Gliwicz, M. Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320:746–748.
- Gozlan, R. E., J. Britton, I. Cowx, and G. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76:751–786.
- Gulati, R., K. Siewertsen, and G. Postema. 1982. The zooplankton: its community structure, food and feeding, and role in the ecosystem of Lake Vechten. Pages 127–163 *in* R. D. Gulati and S. Parma (editors). *Studies on Lake Vechten and Tjeukemeer, The Netherlands*. Springer, Dordrecht, The Netherlands.
- Haney, J., M. Aliberti, E. Allan, S. Allard, D. Bauer, W. Beagen, S. Bradt, B. Carlson, S. Carlson, U. Doan, J. Dufresne, W. Travis Godkin, S. Greene, A. Kaplan, E. Maroni, S. Melillo, A. L. Murby, J. L. Smith Nowak, B. Ortman, J. E. Quist, S. Reed, T. Rowin, M. Schmuck, R. S. Stemberger, and B. Travers. 2013. An image-based key to the zooplankton of North America. Version 5.0. Center for Freshwater Biology, University of New Hampshire, Durham, New Hampshire. (Available from: <http://cfb.unh.edu/cfbkey/html/>)
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Jankowski, T., D. M. Livingstone, H. Bührer, R. Forster, and P. Niederhauser. 2006. Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: implications for a warmer world. *Limnology and Oceanography* 51:815–819.
- Jassby, A. D., T. M. Powell, and C. R. Goldman. 1990. Interannual fluctuations in primary production: direct physical effects and the trophic cascade at Castle Lake, California. *Limnology and Oceanography* 35:1021–1038.
- Killgore, K. J., and J. J. Hoover. 2001. Effects of hypoxia on fish assemblages in a vegetated waterbody. *Journal of Aquatic Plant Management* 39:40–44.
- Komsta, L. 2013. mblm: median-based linear Models. R package version 0.12. (Available from: <https://CRAN.R-project.org/package=mblm>)
- Kraemer, B. M., O. Anneville, S. Chandra, M. Dix, E. Kuusisto, D. M. Livingstone, A. Rimmer, S. G. Schladow, E. Silow, and L. M. Sitoki. 2015. Morphometry and average temperature affect lake stratification responses to climate change. *Geophysical Research Letters* 42:4981–4988.
- Krebs, C. J. 1998. *Ecological Methodology*. 2<sup>nd</sup> edition. Benjamin Cummings, New York.
- Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* 3:21–27.
- Lepak, J. M., C. E. Kraft, and B. C. Weidel. 2006. Rapid food web recovery in response to removal of an introduced apex predator. *Canadian Journal of Fisheries and Aquatic Sciences* 63:569–575.
- Levin, S. A., and J. Lubchenco. 2008. Resilience, robustness, and marine ecosystem-based management. *BioScience* 58:27–32.
- Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecological Applications* 7:1024–1038.
- Mallin, M. A., V. L. Johnson, S. H. Ensign, and T. A. MacPherson. 2006. Factors contributing to hypoxia in rivers, lakes, and streams. *Limnology and Oceanography* 51:690–701.
- Menking, K. M., D. M. Peteet, and R. Y. Anderson. 2012. Late-glacial and Holocene vegetation and climate variability, including major droughts, in the Sky Lakes region of southeastern New York State. *Palaeogeography, Palaeoclimatology, Palaeoecology* 353–355:45–49.
- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76:2347–2360.
- Olson, M. H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. *Ecology* 77:179–190.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:483–488.
- Paerl, H. W., J. L. Pinckney, J. M. Fear, and B. L. Peierls. 1998. Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River Estuary, North Carolina, USA. *Marine Ecology Progress Series* 166:17–25.
- Pagnucco, K. S., G. A. Maynard, S. A. Fera, N. D. Yan, T. F. Nalepa, and A. Ricciardi. 2015. The future of species invasions in the Great Lakes–St. Lawrence River basin. *Journal of Great Lakes Research* 41:96–107.
- Persson, L., A. M. De Roos, D. Claessen, P. Byström, J. Lövgren, S. Sjögren, R. Svanbäck, E. Wahlström, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. *Proceedings of the National Academy of Sciences of the United States of America* 100:4035–4039.
- Pimm, S. L. 1987. Determining the effects of introduced species. *Trends in Ecology and Evolution* 2:106–108.
- Post, D. M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology* 84:1298–1310.



- Post, D. M., J. F. Kitchell, and J. R. Hodgson. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2588–2600.
- Rempfer, J., D. M. Livingstone, C. Blodau, R. Forster, P. Niederhauser, and R. Kipfer. 2010. The effect of the exceptionally mild European winter of 2006–2007 on temperature and oxygen profiles in lakes in Switzerland: a foretaste of the future? *Limnology and Oceanography* 55:2170–2180.
- Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83:263–282.
- Richardson, D. C., D. M. Charifson, B. A. Davis, M. J. Farragher, B. S. Krebs, E. C. Long, M. Napoli, and B. A. Wilcove. 2018. Watershed management and underlying geology in three lakes control divergent responses to decreasing acid precipitation. *Inland Waters* 8:70–81.
- Richardson, D. C., D. M. Charifson, V. J. Stanson, E. M. Stern, J. E. Thompson, and L. A. Townley. 2016. Reconstructing a trophic cascade following unintentional introduction of golden shiner to Lake Minnewaska, New York, USA. *Inland Waters* 6:29–33.
- Richardson, D. C., L. A. Kaplan, J. D. Newbold, and A. K. Aufdenkampe. 2009. Temporal dynamics of seston: a recurring nighttime peak and seasonal shifts in composition in a stream ecosystem. *Limnology and Oceanography* 54:344–354.
- Ruesink, J. L. 2005. Global analysis of factors affecting the outcome of freshwater fish introductions. *Conservation Biology* 19:1883–1893.
- Sarnelle, O. 2005. *Daphnia* as keystone predators: effects on phytoplankton diversity and grazing resistance. *Journal of Plankton Research* 27:1229–1238.
- Schindler, D. E., J. E. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, and K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. *Transactions of the American Fisheries Society* 122:756–772.
- Sereda, J. M., J. J. Hudson, W. D. Taylor, and E. Demers. 2008. Fish as sources and sinks of nutrients in lakes. *Freshwater Biology* 53:278–289.
- Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't!—population crashes of established introduced species. *Biological Invasions* 6:161–172.
- 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.
- Smiley, D., and P. C. Huth. 1983. Fish disappearance in the Northern Shawangunks between 1862 and 1982. Mohonk Preserve, Inc., New Paltz, New York.
- Sommer, U., and H. Stibor. 2002. Copepoda–Cladocera–Tunicata: the role of three major mesozooplankton groups in pelagic food webs. *Ecological Research* 17:161–174.
- Søndergaard, M., T. L. Lauridsen, L. S. Johansson, and E. Jepsen. 2017. Repeated fish removal to restore lakes: case study of Lake Væng, Denmark—two biomanipulations during 30 years of monitoring. *Water* 9:43.
- Tillmanns, A. R., A. E. Wilson, F. R. Pick, and O. Sarnelle. 2008. Meta-analysis of cyanobacterial effects on zooplankton population growth rate: species-specific responses. *Fundamental and Applied Limnology – Archiv für Hydrobiologie* 171:285–295.
- Vander Zanden, M. J., G. J. Hansen, S. N. Higgins, and M. S. Kornis. 2010. A pound of prevention, plus a pound of cure: early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* 36:199–205.
- Vanni, M. J., and C. D. Layne. 1997. Nutrient recycling and herbivory as mechanisms in the “top–down” effect of fish on algae in lakes. *Ecology* 78:21–40.
- Vrede, T., A. Ballantyne, C. Mille-Lindblom, G. Algesten, C. Gudasz, S. Lindahl, and A. K. Brunberg. 2009. Effects of N : P loading ratios on phytoplankton community composition, primary production and N fixation in a eutrophic lake. *Freshwater Biology* 54:331–344.
- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052.
- Williamson, C. E., E. P. Overholt, R. M. Pilla, T. H. Leach, J. A. Brentrup, L. B. Knoll, E. M. Mette, and R. E. Moeller. 2015. Ecological consequences of long-term browning in lakes. *Scientific reports* 5:18666.
- Wu, L., and D. A. Culver. 1991. Zooplankton grazing and phytoplankton abundance: an assessment before and after invasion of *Dreissena polymorpha*. *Journal of Great Lakes Research* 17:425–436.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16:454–459.