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The effects of surface water warming on nutrient limitation of phytoplankton in headwater lakes of the Hudson River

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Experimental incubations for nutrient limitation (L) and Lake Minnewaska (R)



Abstract

In New York State, lake ecosystems provide drinking water, food, and recreation. However, lakes are susceptible to harmful indirect effects like climate change. Additionally, many lakes in New York State have been experiencing increasing nutrient loads, even those residing in protected lands. There continues to be debate surrounding which type of nutrient - nitrogen or phosphorus - is the primary determinant of productivity and is the cause of algal blooms. As a result, there is a critical need to understand the interactive effects between climate change and nutrient limitation of phytoplankton. To test this interaction, we used the 'Sky Lakes' located on the northern Shawangunk Ridge within managed lands. We surveyed three Sky Lakes to examine variability in trophic status. We used experimental incubations to determine nutrient limitation status of the study lakes. Finally, we used replicate experimental incubations to examine nutrient limitation under warming conditions. We found that all three lakes were colimited by both nitrogen and phosphorus. Under warming scenarios, nutrient limitation status stayed the same but the colimitation effect size increased. Local managers and governments need to consider both nitrogen and phosphorus management strategies for algal blooms, especially with a rapidly changing climate.

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Three Summary Points of Interest

- Lake phytoplankton biomass was colimited by both nitrogen and phosphorus in 1 week incubations.
- Under warming scenarios, nutrient limitation status stayed the same but biomass increased.
- Freshwater resource managers need to consider both nitrogen and phosphorus management strategies for algal blooms, especially with a rapidly changing climate.

Keywords

Climate change; nutrient limitation, phytoplankton, lakes

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Introduction

As a result of climate change, the Hudson River Valley has experienced increases in air temperatures and some of the greatest increases in precipitation and extreme storm events in the country (Melillo et al. 2014). In recent work that includes multiple lakes in the Hudson River watershed, Richardson et al. (2017) found that lake temperature during peak stratification in northeastern North America is changing faster than other regions of the world due to climate forcing and corresponding changes in air temperature and precipitation patterns. In general, 90% of lakes had warming surface waters and increasing stratification during summers. During a previous NYS WRI funded project, we analyzed the warming patterns in Mohonk Lake, one of the focal lakes for this study. Surface temperatures were warming at $\sim 0.5^{\circ}\text{C}$ per decade over the last 33 years. The stability of thermal stratification, integrated over the course of the entire stratified period, increased by $\sim 44\%$ over the 33-year history.

This warming and increased stratification affects lake physics and internal heat distribution. Subsequently, there is a variety of potential ecosystem-level consequences with concomitant impacts on ecosystem services. Lake warming results in lengthening of the stratification period with shorter ice cover periods (Benson et al. 2012). Across lakes of different trophic status, this may exacerbate extent and duration of hypolimnetic anoxic conditions leading to the loss of aquatic biota and changes in water chemistry (Palmer et al. 2014). In many lakes, anoxic conditions will free phosphorus bound in lake sediments, and, combined with changes in lake mixing regimes, will result in changes to nutrient dynamics and ultimately lake productivity (Verburg and Hecky 2009). Increasingly warm surface temperatures could favor harmful cyanobacterial algal blooms and transition lakes towards eutrophic conditions (Paerl and Paul 2012). Warming and increasingly anoxic deepwater can both result in increases cyanobacterial recruitment in species that overwinter in and draw phosphorus from the sediments (e.g., Cottingham et al. 2015).

Nitrogen (N) and phosphorus (P) are natural components of lake ecosystems but, when in excess, are the major pollutants that drive algal blooms. Use of N- and P-based fertilizers, combustion of fossil fuels,

agricultural runoff, and other anthropogenic impacts have led to increased N and P concentrations within aquatic systems (Vitousek, 1997; Bennett et al. 2001). These additions have been shown to increase productivity in lakes, leading to eutrophication, loss of biodiversity, toxic cyanobacterial blooms, and loss of aesthetic or recreational value (Kolzau et al. 2014). However, there continues to be debate surrounding which nutrient - N or P - is the primary determinant of productivity in lake ecosystems (Schindler et al. 2008). More recently there has been increased emphasis on the importance of co-limitation by N and P (Elser et al. 2007; Pearl et al. 2016). Nutrient limitation type is essential in light of this continuing debate and the need to prevent human and ecological consequences of eutrophication.

In this report, we address how the interaction between indirect effects (climate change) and direct effects (nutrient loading) could drive algal blooms in headwater lakes. We used experimental examination of nutrient limitation across different lakes along the Shawangunk Ridge with varying nutrient concentrations and trophic status. We also used replicate experimental incubations at two different temperatures to examine the effects of increased temperature on nutrient limitation.

Results & Discussion

The three study lakes were glacially-formed and are primarily rain-fed with small watersheds and minimal groundwater exchange (Caine et al. 1991). Each lake's watershed is underlain by erosion resistant quartz conglomerate and sandstone; Mohonk is an exception with an inlier of Martinsburg shale within the quartz conglomerate (Menking et al. 2012). Minnewaska is close to neutral because of buffering by gravel hiking trails, Awosting is acidic as a result of acid rain, and Mohonk is neutral due to the shale inlier that acts as a buffer (Table 1, Richardson et al. 2018). Despite being close in proximity (~ 10 km), the three lakes differ in their food webs. Minnewaska has been fishless since the 1920s because of acid rain and low lake pH (Smiley and Huth 1983). With a more recent increase in pH (Richardson et al. 2018), the lake became viable for fish survival and reproduction around 2005. In 2008, Golden shiners (*Notemigonus crysoleucas*, a small minnow) were unintentionally introduced to Minnewaska (Charifson et al. 2015). As a result, a trophic cascade occurred with

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algal blooms and a shift from oligotrophy to mesotrophy in 2011 (Richardson et al. 2016). Largemouth bass (*Micropterus salmoides*) were subsequently introduced in 2012, also unintentionally (Charifson et al. 2015). As of 2014, shiners were extirpated from the lake, likely as a result from bass predation (Charifson et al. 2015). Awosting is an oligotrophic, clear-water lake with no fish observed in the previous 100 years (Smiley and Huth 1983). Mohonk is a mesotrophic lake and contains a diverse fish community including shiners, largemouth bass, and other various species of sunfish, bass, and trout (Smiley and Huth 1983). Landowners who operate the lakeside hotel have stocked fish in Mohonk for recreation since 1871 (Smiley and Huth 1983). These geologic and food web differences explain the variability in nutrient concentrations and algal biomass (Table 1).

Table 1. Biological and chemical characteristics of the three study lakes: Minnewaska (Minn), Awosting (Awos), and Mohonk (Mohk). Chlorophyll *a* concentrations (Chl *a*), Secchi depth (Secchi), total nitrogen concentration (TN), and total phosphorus concentration are presented from synoptic sampling at the start of the first experiment on 19Jun2018.

Lake	Chl <i>a</i> (µg/L)	pH	Secchi (m)	TN (µg/L)	TP (µg/L)
Minn	1.1	6.9	6.7	100	4
Awos	0.1	5.5	3.6	70	4
Mohk	2.8	6.4	7.3	120	8

We completed nutrient limitation experiments for all three lakes from 19 Jun 2018 to 26 Jun 2018; all incubations took place in Minnewaska to standardize temperature and light exposure. We used chlorophyll *a* (chl *a*) concentrations as the response variable and as a proxy for algal biomass in all experiments. For Minnewaska, there were significant main effects for both P ($F_{1,12}=12$, $p=0.004$) and N ($F_{1,12}=8$, $p=0.016$) and a significant interaction effect ($F_{1,12}=23$, $p<0.001$). This indicated that Minnewaska phytoplankton were colimited by both N and P (Fig. 1, top). For Awosting, neither main effects were significant ($p>0.05$) but there was a significant interaction effect ($F_{1,12}=95$, $p<0.001$). This indicated that Awosting phytoplankton were colimited by both N and P (Fig. 1, middle). For Mohonk, there was no significant main effect for P ($p>0.05$), but

there was a significant main effect for N ($F_{1,12}=7.3$, $p=0.02$). There was also a significant interaction effect ($F_{1,12}=55$, $p<0.001$). This indicated that Mohonk phytoplankton were colimited by both N and P with serial limitation with N as the primary limiting nutrient and P as the secondary limiting nutrient (Fig. 1, bottom). The N+P treatment response ratios were 4.8, 4.0, and 3.0 for Minnewaska, Awosting, and Mohonk, respectively.

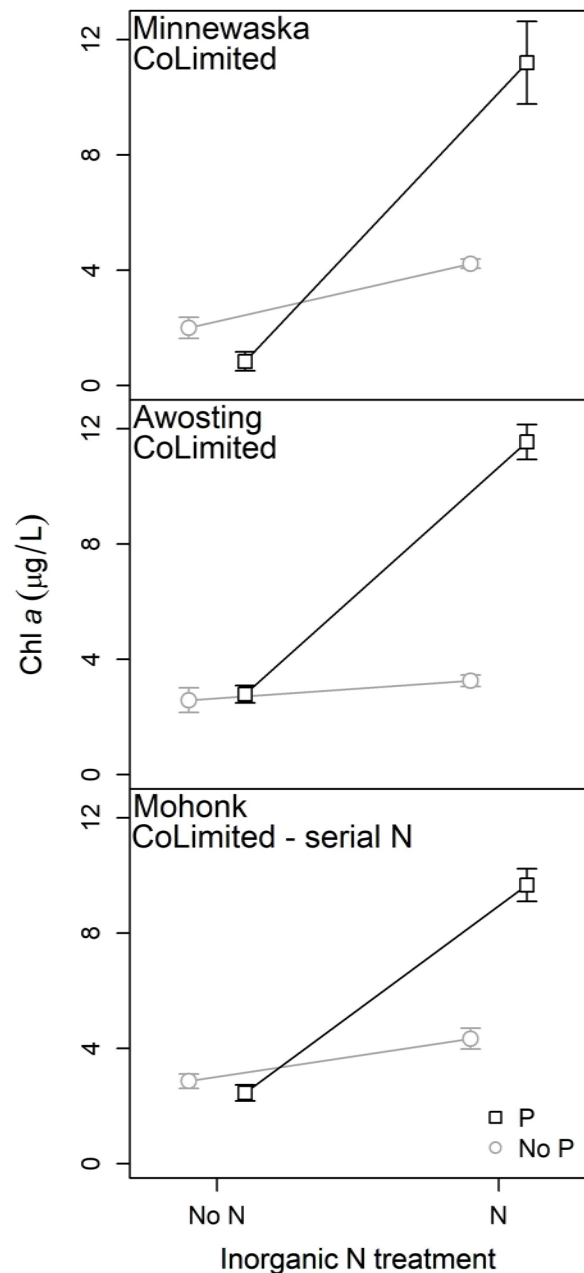


Figure 1. Nutrient limitation experiments from 19Jun2018 to 26Jun2018 from three Sky Lakes on the

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northern Shawangunk Ridge. Chlorophyll a (chl a) was used as a proxy for algal biomass and compared across nutrient treatments. Both Minnewaska (top) and Awosting (middle) were colimited, while Mohonk (bottom) was colimited with N as the primary nutrient of limitation and P as the secondary nutrient of limitation (serial N).

In all three lakes, there was a synergistic increase in productivity and colimitation from both N and P (Fig. 1), an increasingly common occurrence in freshwater lakes (e.g., Elser et al. 2009; Muller and Mitrovic 2015; Paerl et al. 2016). The prevalence of colimitation could be facilitated by two mechanisms that are not mutually exclusive. First, additional nutrients of one type could allow individual phytoplankton cells to access other nutrients that were previously unavailable. For example, additional N may allow the production of N-rich enzymes (e.g., phosphatase) that facilitate access to P (Bracken et al. 2015). Second, colimitation can be facilitated at the community level when various taxa within the community are limited by different nutrients; this can especially occur in lakes with diverse phytoplankton communities that include N-fixing taxa (Harpole et al. 2011; Muller and Mitrovic 2015). In these lakes, algal biomass was low (Table 1) and phytoplankton diversity is high when phytoplankton biomass is low which may lead to higher likelihood of taxa with colimitation or coexistence of taxa that favor N or P. Additionally, other

In the second experiment, we incubated Mohonk phytoplankton communities under two conditions: first, in Lake Minnewaska with baseline lake temperatures experienced by those phytoplankton and in our local campus pond where the shallower and more urban environment contributed to warmer conditions. The temperatures in the campus pond followed similar diel

dynamics as the lake but were consistent warmer over the course of the experiment (Fig. 2). The average difference over the course of the experiment was 3.8°C. This is proportional to warming that could be seen in New York lakes within the next century (Richardson et al. 2017).

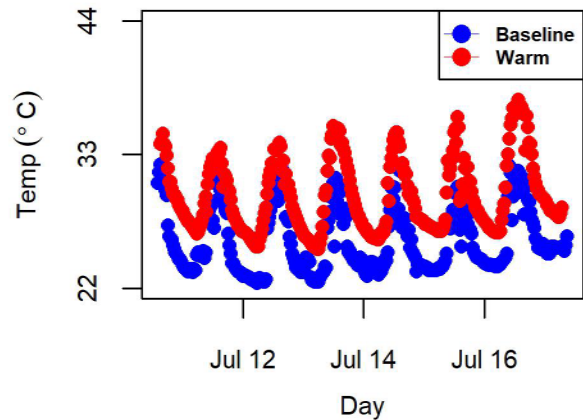


Figure 2. Comparison of temperature for incubations in warm and baseline conditions. The mean temperature for the baseline was 25.9°C; the mean temperature for the warm scenario was 29.7°C over the course of the incubation for a difference of 3.8°C.

Both incubations yielded similar results for nutrient limitation. Under a warming scenario, there was no significant main effect for P ($p > 0.05$), but there was a significant main effect for N ($F_{1,12} = 5.4$, $p = 0.04$). There was also a significant interaction effect ($F_{1,12} = 69.2$, $p < 0.001$). This indicated that under warming temperatures, Mohonk phytoplankton were colimited by both N and P with serial limitation with N as the primary limiting nutrient and P as the secondary limiting nutrient (Fig. 3 top). Under baseline conditions, there was no significant main effect for P ($p > 0.05$), but there was a significant main effect for N ($F_{1,12} = 7.9$, $p = 0.02$). There was also a significant interaction effect ($F_{1,12} = 65.0$, $p < 0.001$). This indicated that under baseline temperatures Mohonk phytoplankton were also colimited by both N and P with serial limitation with N as the primary limiting nutrient and P as the secondary limiting nutrient (Fig. 3 bottom). The response ratio for the N+P treatment in the warming scenario was 4.2; the response ratio for the N+P treatment in the baseline scenario was 3.9. This indicates an 8% increase in the

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phytoplankton response for the nitrogen and phosphorus treatment under warming conditions.

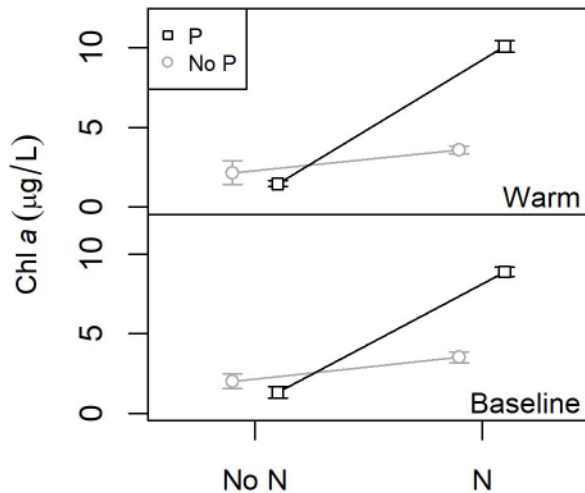


Figure 3. Nutrient limitation experiments from Mohonk phytoplankton communities incubated in warmer (top) and baseline (bottom) conditions from 10Jul2018 to 17Jul2018. Chlorophyll a (chl a) was used as a proxy for algal biomass and compared across nutrient treatments. No P and P indicate phosphorus amendments and No N vs. N indicate inorganic nitrogen amendments as nitrate and ammonium.

Throughout the world, freshwater lakes are warming rapidly (O'Reilly et al. 2015) and especially in the New York and northeastern United States region (Richardson et al. 2017). The warming surface water has widespread implications for lake ecosystem function (Adrian et al. 2009) and particularly for phytoplankton communities. Phytoplankton may bloom earlier and the community composition may change with a loss of biodiversity (Elliott 2012). For example, a 3°C rise in temperature will result in a shift towards small-sized phytoplankton and cyanobacteria, small photosynthesizing bacteria (Rasconi et al. 2015). The shift towards these organisms are particularly troubling because of their ability to produce toxins that are harmful to human health (see Elliot 2012). In this study, we did not focus on any particular taxa but saw an overall increase in the combined response to N and P (Fig. 3). As internal and external nutrient loading increases in addition to warming lakes, our results indicate the possibility of

additive or synergistic effects on phytoplankton. Examining the particular phytoplankton taxa that were driving this increase would be important in understanding implications for human ecosystem goods and services.

Policy Implications

Algal blooms in freshwater lakes are expanding in our region and worldwide (Pearl et al. 2011; Lurling et al. 2017). Traditionally, the paradigm that P limits phytoplankton growth in freshwater lakes has controlled lake manager strategies and policies that target reductions in external P loading to lakes (Lewis and Wurtsbaugh 2008). However, this study and others demonstrate the importance of considering N simultaneously with P when considering effective management strategies. At timescales that are most relevant to the development and persistence of single algal bloom events, Colimitation is especially important (Harpole et al. 2011). In New York State, there has been a recent focus on harmful algal blooms (HABs) in lakes; [see the Department of Environmental Conservation page here](#). The NY State government has targeted 12 priority water bodies with a focus on developing and implementing action plans to combat HABs – many of these waterbodies are critical water supplies or recreational lakes. We advocate for comprehensive strategies that are grounded in science, monitoring, and account for simultaneous management of multiple nutrients that might control HABs.

Methods

Our three study lakes, Lake Minnewaska, Lake Awosting, and Mohonk Lake, are located on the Shawangunk Ridge, mid-Hudson Valley, New York, USA (Table 2). They are small lakes with similar depth and surface area (Table 2).

Synoptic field survey: We surveyed the Sky Lakes of the northern Shawangunk Ridge (Fig. 1) throughout the stratified period. We completed a synoptic survey where we visited all 3 lakes within one single day to eliminate any effects due to weather events. We measured trophic state indices (chl a concentrations, Secchi depth, and total nitrogen and phosphorus concentrations) as well as conductivity, dissolved organic carbon, and pH at the deepest location of each lake at the surface and in the hypolimnion. We sampled

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temperature and dissolved oxygen profiles to look for thermal stratification and hypoxia.

Table 2. Location and geomorphological characteristics of the three study lakes: Minnewaska (Minn), Awosting (Awos), and Mohonk (Mohk). Latitude (Lat), Longitude (Long), maximum depth (Max Depth), mean depth, and surface area are presented.

Lake	Lat (°N)	Long (°W)	Max Depth (m)	Mean Depth (m)	Surface Area (ha)
Minn	41.73	-74.24	23	5.7	13.8
Awos	41.71	-74.29	29	5.0	39.0
Mohk	41.77	-74.16	19	6.0	6.9

In situ experiments: To measure nutrient limitation of phytoplankton communities from the epilimnion in each of our three study lakes, we used two in situ microcosm incubations with excess nutrient addition (methods from Williamson et al. 2010). In short, we collected water from each lake using a Van Dorn sampler and filtered through 125 µm mesh to remove zooplankton. We prepared sixteen 500 mL mesocosms (6" x 6" Bitran bags, Fisher Scientific, USA) for each lake with four replicates assigned to each of the following four treatments: control (no amendments), +N alone (increased nitrate, NO₃⁻ as NaNO₃, and ammonium, NH₄⁺; as NH₄Cl, by 168 µg/L each above background), +P alone (increased phosphate, PO₄³⁻ as NaH₂PO₄, by 31 µg/L), and +N+P combined. We standardized amendments to ensure that nutrient addition would elicit a response from the most nutrient-rich study lake. All mesocosms were randomly positioned on floating PVC racks and were covered with neutral-density filters to minimize photoinhibition. The filters reduced incident light exposure by about two thirds~66% making experimental treatments more similar to underwater light exposures. We analyzed chl *a* concentration as a proxy for phytoplankton biomass using standard hot ethanol techniques in the lab.

We completed two experiments using the above protocols. First, we incubated phytoplankton communities from all three study lakes (Minnewaska, Awosting, and Mohonk) at the top of Lake Minnewaska in order to standardize light and temperature between experimental groups for one week (19 Jun 2018 to 26

Jun 2017). To test the effects of climate change, we replicated the exact same experiment with Mohonk lake phytoplankton in two ways: first, the same incubation at the top of Lake Minnewaska representing baseline lake temperatures for algal community and, second, incubation in a shallower and therefore warmer pond on the SUNY New Paltz campus to simulate warmer lake conditions. These incubations took place from 10Jul2018 to 17Jul2018. We used Onset HOBO loggers within two randomized bags and record temperature and light throughout the two incubations.

For each lake experiment, we performed a two-way ANOVA to analyze the change in chl *a* with N or P amendments (presence/absence) as factors. All statistical analyses were conducted in R software. If chl *a* concentrations across interaction treatment levels had heterogeneous variances (Bartlett test, $p < 0.05$), we log-transformed data prior to running the ANOVA. Based on the interaction and main effects, we determined if there was no nutrient limitation, single factor limitation, colimitation, or colimitation with N or P primary limitation (as per Tank and Dodds 2003). We calculated the colimitation effect size as the response ratio between the mean chl *a* concentration from the NP treatment and the sum of the mean chl *a* concentrations from N, P, and C treatments with a correction for the number of means being compared (Eq. 1).

$$RR_{NP} = \left(\frac{3\overline{NP}}{\overline{C} + \overline{N} + \overline{P}} \right) \quad (\text{Eq. 1})$$

Outreach Comments

We interact on a regular basis with the local managers of our study lakes including Minnewaska State Park (New York State park), Mohonk Preserve (non-profit NGO), and Mohonk Mountain House (business). We present findings, collaborate with government scientists, and advise on management plans and strategies.

This project also relates to a grassroots organization that we helped co-found: NE GLEON (Northeastern North America branch of the Global Lakes Ecological Observatory Network, GLEON, <http://gleon.org/>) which was conceived at the 16th GLEON all-hands meeting in Québec, Canada out of a desire to increase interactions among scientists in our lake-rich region and to engage

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undergraduates in team science. Our network of >10 lab groups is led by an informal planning committee and our activities over the past 3 years have resulted in increased undergraduate participation in buoy science, several funding initiatives, and cross-site experiments. Our signature event is an annual 2-day conference for 25-35 undergraduates, graduate students, and primary investigators held at the Cary Institute of Ecosystem Studies each April. One outcome of the first conference was a protocol for conducting cross-site mesocosm experiments – the data from this report contributes to that overall study across 27 lakes in our region that is currently being analyzed.

We also created a 5-minute animated documentary titled 'Algal Growth in Freshwater Lakes' to bring our research to a wider audience at a broad level. [Click here for the video](#). We will forward this documentary to our community partners locally and across the state and post on social media for widespread dissemination.

Student Training

This grant directly funded one undergraduate researcher (Heather Wander, SUNY New Paltz, Biology, '18) for summer research; Heather continued working in fall 2019 on this project as an independent study student. This grant also supported two graphic design students (Olivia Carlen and Luke Barnell, SUNY New Paltz Graphic Design, '19) to create one short documentary in spring 2019, see above. Additionally, Richardson had multiple other undergraduate students (Kari Dawson, Winston-Salem State University, '19; Sabrina Volponi, Bridgewater College '20; Vanessa Morgan, SUNY New Paltz '20; Brenna O'Brien, SUNY New Paltz '20) from various intra- and extra-mural grants as interns and independent study students working on various facets of his Sky Lakes project during the summer and school year. The students were trained in the field and lab as careful and diligent ecologists. They learned how multiple field and lab techniques, data analyses, and scientific communication. Additionally, all undergraduate researchers developed an 'elevator pitch,' or a short one-minute summary of their research that they used to explain to their friends, family, and other inquisitive parties, especially state park employees and recreational visitors. The short documentaries provided training for the Olivia and Luke

to practice their craft, co-develop as scientific script, and work with the scientists as "employers."

Publications/Presentations

Wander HL*, Carter E*, Tracy A*, Katayama T*, Volponi S*, Yokota K, Arnott S, Ewing H, Norman B, Morales MA, Williams CJ, Ward N, Brentrup JA, Wigdahl-Perry CR, Holeck KT, Bruesewitz DA, Richardson DC. Inorganic nitrogen, organic nitrogen, and phosphorus limitation of lake phytoplankton and heterotrophs across northeastern North America. Global Lake Ecological Observatory Network meeting G20 poster presentation, Rottneest Island, Australia.

Additional final reports related to water resource research are available at <http://wri.cals.cornell.edu/news/research-reports>

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