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ALTERATIONS IN YELLOWSTONE LAKE NITROGEN CYCLING DUE TO INTRODUCED LAKE TROUT AND SUBSEQUENT DECLINE OF YELLOWSTONE CUTTHROAT TROUT

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+ ABSTRACT

Invasive species may alter processes by indirectly affecting other species in the ecosystem, but indirect affects are difficult to measure and often pre-invasion data were not collected. However, models may be used with empirical relationships and available past data to reconstruct past processes. The introduction of lake trout (Salvelinus namaycush) in Yellowstone Lake may have indirect effects on nitrogen cycling and provide an opportunity to study the effects of an invasive species on lake processes. To estimate how lake trout altered nitrogen cycling in Yellowstone Lake, we measured ammonium (NH$_4^+$) uptake by phytoplankton in 2005 and estimate past NH$_4^+$ uptake using empirical relationships and past data. Using $^{15}$N, we measured phytoplankton uptake in 4 areas of Yellowstone Lake. Phytoplankton demanded 4.9 mg N m$^{-2}$ hr$^{-1}$ during the ice-free season of 2005. Uptake was higher at warmer water temperatures and shallower Secchi disk depths (measure of phytoplankton biomass). Using relationships among uptake, water temperature, and Secchi disk depth, we estimated phytoplankton uptake in the past based on historical Secchi disk depths and water temperatures. Water temperatures have increased 0.29°C/decade and Secchi disk depths became 0.53 m/decade deeper over the past 30 years. Using our multiple regression model, phytoplankton uptake did not change between 1976 and 2006. The interaction between warmer water temperatures and deeper Secchi disk depths (a sparser algal assemblage) cancelled out resulting in no changed in modeled uptake. Therefore, when estimating past processes, we should use multiple predictors.

+ INTRODUCTION

The introduction of invasive species and climate change threaten to alter ecosystems around the globe; however, many times their effects on ecosystems are unknown, but potentially large. Invasive species threaten to homogenize biota (Rahel 2000), alter biodiversity (Lonsdale 1999, Randall 2000), change interactions among species (Ruzyczki et al. 2003), and modify ecosystem structure and function (Tronstad 2008). Climate change was single handedly responsible for changes in species ranges (Parmesan and Yohe 2003), earlier annual events (Winder and Schindler 2004), and temperatures (Walther et al. 2002). However, the combined effects of invasive species and climate changed have rarely been investigated.

Of particular concern is the interaction between climate change and invasive species (Dukes and Mooney 1999, Stachowicz et al. 2002). Predicting the response of ecosystems to a single stressor is complicated, and invasive species and climate change may interact in...
surprising ways. Together invasive species and climate change may be additive or multiplicative; however, the answer remains largely uninvestigated (Dukes and Mooney 1999). One exception is Stachowicz et al. (2002) who found that the growth rate and recruitment of invasive sessile marine invertebrates was higher than native invertebrates at higher temperatures, suggesting that climate change facilitated invasive species introductions. Our study investigated how climate change and invasive species simultaneously affected nutrient uptake in Yellowstone Lake.

Ideally, time series data are used to tease apart the effects of invasive species and climate change; however, often data were not collected through time. To estimate how invasive species and climate change interact, we can use models. Models do not replace historical data, but they can be useful to estimate changes.

The introduction of lake trout (Salvelinus namaycush) in Yellowstone Lake provided an opportunity to investigate the combined effect of invasive species and climate change. Previous studies demonstrated that lake trout indirectly altered phytoplankton biomass in Yellowstone Lake (Tronstad 2008). However, the indirect effect of lake trout on phytoplankton uptake was unknown. Phytoplankton uptake had not previously been measured in Yellowstone Lake, therefore, past nitrogen demand by phytoplankton is unknown. However, using empirical relationships, and past water temperature and Secchi disk depths (measure of phytoplankton biomass), we estimated past phytoplankton uptake. Our objective was to quantify current phytoplankton uptake of nitrogen and estimate uptake in the past.

**Study Site**

Yellowstone Lake is located on the Yellowstone Plateau, Wyoming, which has a cold, continental climate with short summers and long winters (Felicietti et al. 2003). Yellowstone Lake is partially located within the Yellowstone caldera, an active silicic volcano (Morgan et al. 2003). Geology of the lake and surrounding basin is mainly rhyolite, with northern and eastern areas composed of andesite (Finn and Morgan 2002). Yellowstone Lake is mesotrophic (Kilham et al. 1996) and ice-covered from December through May (Gresswell and Varley 1988). Yellowstone Lake is the largest high-elevation (2357 m) lake in North America (Gresswell et al. 1997), with a surface area of 341 km², shoreline length of 239 km, and average depth of 43 m (Kaplinksi 1991). The lake is dimictic with summer stratification occurring from mid-July to mid-September with a deep (~20 m) epilimnion. During the ice-free season, surface water temperatures vary between 3°C after ice-off and 18°C in mid-summer, dissolved oxygen ranges between 7 and 11 mg/L, slightly basic pH (7.2 to 8.3), and low water electrical conductivity (69 to 96 µS/cm; J. Arnold, unpublished data).

Yellowstone Lake contained the largest remaining lacustrine population of Yellowstone cutthroat trout (Varley and Gresswell 1988), but their abundance fluctuated through time. The number of spawning cutthroat trout was low in the 1940s and 1950s due to egg-taking and liberal creel limits; however, the cutthroat trout population recovered after egg-taking ceased and stringent creel limits were imposed. The number of spawning cutthroat trout was high in the 1970s and 1980s, averaging 48,000 fish spawning annually in Clear Creek, a tributary stream on the east side of Yellowstone Lake. The number of cutthroat trout peaked in 1978 when 70,105 fish spawned in Clear Creek. However, the abundance of cutthroat trout declined by 60% in Yellowstone Lake and 99% in Clear Creek since 1990 (Koel et al. 2005). Presently, indices of cutthroat trout abundance are the lowest on record.

Several fish species have been introduced in Yellowstone Lake, and longnose sucker (Catostomus catostomus), redside shiner (Richardsonius balteatus), lake chub (Couesius plumbeus), and lake trout (Salvelinus namaycush) have reproducing populations (Gresswell and Varley 1988, Gresswell et al. 1997). Lake trout are the only piscivorous fish in Yellowstone Lake. Even as young fish, only a small proportion of lake trout diet is zooplankton (Ruzyczki et al. 2003) Lake trout were illegally introduced into Yellowstone Lake (Kaeding et al. 1996) in ~1985 (Munro et al. 2005) and they eat ~41 cutthroat trout per year (Ruzyczki et al. 2003). Lake trout are found throughout the water column after ice-out, but live primarily in the depths of Yellowstone Lake during summer. In fall, these fish spawn in shallow areas of Yellowstone Lake. The National Park Service (NPS) actively remove lake trout using gill nets, electrofishing, and a must kill angler restriction to reduce predation on native cutthroat trout.
(Koel et al. 2005). Between 1994 and 2006, the NPS removed >198,000 lake trout from the lake (Koel et al. 2007).

Other threats to cutthroat trout include whirling disease and drought. Whirling disease was discovered in 1998 and mainly affects young of the year cutthroat trout in certain spawning streams (Koel et al. 2006). For example, whirling disease has decimated the spawning run to Pelican Creek, a tributary with organic substrates that is preferred by the tubificid host, *Tubifex tubifex* (Krueger et al. 2006). Only 11% of cutthroat trout in Yellowstone Lake were infected with whirling disease (Koel et al. 2006). However, the number of spawning cutthroat trout has drastically declined in streams not affected by whirling disease. Therefore, we attributed the decline of cutthroat trout primarily to lake trout predation. On-going drought also affects young of the year cutthroat trout in small tributary streams by stranding individuals (Koel et al. 2005).

**METHODS**

To quantify the current demand for \( \text{NH}_4^+ \) in Yellowstone Lake, we measured \( \text{NH}_4^+ \) uptake by pelagic microbes (i.e., algae and bacteria). We estimated microbial \( \text{NH}_4^+ \) uptake by incubating \( ^{15}\text{N}\text{H}_4\text{Cl} \) in 2.5 L Nalgene polycarbonate bottles for 3 hours in early June, late July, and early October 2005. We collected water at 5, 10, and 15 m depths from 4 areas (South Arm, Southeast Arm, east of Stevenson Island, and West Thumb) of Yellowstone Lake (2 to 3 bottles per depth per site) and incubated bottles at their respective depths in northern Yellowstone Lake. To minimize uptake after incubations, we kept water samples dark and on ice. We collected phytoplankton by filtering 1.2 L of water through ashed 25-mm PALL type A/E glass fiber filters (~1 µm pore size) at 3 stages in the experiment: before adding \( ^{15}\text{NH}_4^+ \) (ambient), immediately after adding \( ^{15}\text{NH}_4^+ \) (t = 0) and after 3 hours of incubating (t = 3 hr). Filters were rinsed with 60-mL of deionized water after filtering microbes to remove excess \( ^{15}\text{N} \) from filter. Samples were analyzed for \( \delta^{15}\text{N} \) (%) and the mass of N (µg) using Thermo-Finnigan Delta plus Advantage gas isotope-ratio mass spectrometer (Waltham, MA) interfaced with a Costech Analytical ECS4010 elemental analyzer (Valencia, California) at the Colorado Plateau Stable Isotopes Laboratory in Flagstaff, Arizona.

To estimate \( \text{NH}_4^+ \) uptake by phytoplankton, we calculated the fraction of \( ^{15}\text{N} \) in each sample \( (\text{AF}; \text{atomic fraction}) \). The amount of \( ^{15}\text{N} \) taken up during the incubation was calculated as the difference in \( \text{AF} \):

\[
AF_{xs} = AF_{t=3hr} - AF_{t=0}
\]

where \( AF_{xs} \) is the \( AF \) excess, \( AF_{t=3hr} \) is the \( AF \) after 3 hours of incubating, and \( AF_{t=0} \) is the \( AF \) at time zero (sample taken immediately after \( ^{15}\text{N} \) was added). Total \( ^{15}\text{N} \) taken up \( \left(^{15}\text{N}_{\text{TU}}; \mu\text{g N L}^{-1} \text{hr}^{-1}\right) \) was calculated by:

\[
^{15}\text{N}_{\text{TU}} = \frac{N_{\text{filter}} \times AF_{xs}}{t \times V}
\]

where \( N_{\text{filter}} \) is the amount of N on the filter (µg), \( t \) is the incubation time (hr), and \( V \) is the volume of water filtered (L). The mass of \( ^{15}\text{N} \) taken up by microbes was calculated as:

\[
M_{\text{TU}} = ^{15}\text{N}_{\text{TU}} \times t
\]

Mean concentration of \( ^{15}\text{N} \) excess in the bottle \( (\text{C}_{^{15}\text{N}}; \mu\text{g} \text{ }^{15}\text{N}/\text{L}) \) was calculated as:

\[
\text{C}_{^{15}\text{N}} = \frac{0.2 - (0.2 - M_{\text{TU}})}{2}
\]

where 0.2 µg \( ^{15}\text{N}/\text{L} \) is the concentration added to each bottle. To calculate the turnover time for an \( \text{NH}_4^+ \) molecule (\( \text{TT}; \text{hr}^{-1} \)), we used:

\[
\text{TT} = \frac{^{15}\text{N}_{\text{TU}}}{\text{C}_{^{15}\text{N}}}
\]

We calculated phytoplankton \( \text{NH}_4^+ \) uptake (µg N m\(^{-3}\) hr\(^{-1}\)) by:

\[
U = \text{TT} \times C_A \times 1000
\]

where \( C_A \) is the ambient concentration of \( \text{NH}_4^+ \) (µg N/L) in Yellowstone Lake water. In addition to microbial uptake, we measured Secchi disk depths (m) at each site and water temperature (°C) at the incubation site.
To estimate changes in past NH$_4^+$ uptake in Yellowstone Lake, we modeled uptake using past Secchi disk depths and water temperatures recorded since 1976 using multiple regression. Secchi disk depths are an index of phytoplankton biomass in Yellowstone Lake (Tronstad 2008) and cutthroat trout indirectly affect phytoplankton biomass through cascading trophic interactions (Tronstad 2008). Temperature represented the effects of climate change on Yellowstone Lake. Because long-term data were available for these variables, we created relationships among Secchi disk depths, water temperature, and NH$_4^+$ uptake from our 2005 measurements. To estimate past NH$_4^+$ uptake, we used historical Secchi disk depths and water temperatures with our empirical relationships from 2005.

**RESULTS**

Pelagic microbes took up more NH$_4^+$ in July (8.1 ± 1.9 mg N m$^{-2}$ hr$^{-1}$; 405 ± 93 µg N m$^{-3}$ hr$^{-1}$), than June (1.6 ± 0.7 mg N m$^{-2}$ hr$^{-1}$; 81 ± 34 µg N m$^{-3}$ hr$^{-1}$) or October (1.6 ± 0.29 mg N m$^{-2}$ hr$^{-1}$; 82 ± 15 µg N m$^{-3}$ hr$^{-1}$; Tukey's: $p < 0.05$) in 2005. Ammonium residence time was shortest in June (9.7 ± 3.9 hr) and July (3 ± 0.6 hr), and longest in October (38 ± 5.8 hr; Tukey's: $p < 0.05$). Because Secchi disk depths and water temperatures were collected in Yellowstone Lake since 1976, we formed empirical relationships between these variables and NH$_4^+$ uptake in 2005. In 2005, deeper Secchi disk depths (SD; m) indicated lower NH$_4^+$ uptake (Fig. 1A). Conversely, higher water temperatures (T; °C) suggested higher NH$_4^+$ uptake (Fig. 1B). Together, Secchi disk depth and water temperature explained 73% of the variation in NH$_4^+$ uptake ($N_{TU}$; µg N m$^{-3}$ hr$^{-1}$) measured in 2005.

$$\ln N_{TU} = 3.68 + 0.29 T - 0.18 SD, \; t_T = 11.6, \; t_{SD} = -5.8, \; P < 0.0001, \; df = 51.$$

We predicted past NH$_4^+$ uptake using the empirical relationship from 2005, and past surface water temperatures and Secchi disk depths (Theriot et al. 1997; Jeff Arnold, unpublished data). Secchi disk depths have become 1.6 m deeper since 1976 (Fig. 2A), indicating lower phytoplankton biomass (Tronstad 2008). Lake temperatures increased 0.29° C/decade during the past 30 years (Fig. 2B):

$$T = -40 + 0.029 y - 0.18 a - 0.86 I + 0.056 a \times I$$

where $y$ is year (e.g., 1976), $a$ is days since August 10th, and $I$ is an indicator variable where 0 is on or before August 10th and 1 is after August 10th. $r^2 = 0.87$, df = 213, $t_y = 3.0$, $t_a = -33$, $t_I = -2.1$, $t_{I \times a} = 5.7$, $P < 0.001$. Water temperature in Yellowstone Lake increased from ice-off to August 10th and decreased thereafter, thus, we regressed inter-annual variation in water temperature...
temperature as days since August 10th. Using these past data, the multiple regression model suggested that microbial uptake in Yellowstone Lake was similar from 1976 to 2005 ($t = -0.06$, df = 215, $r^2 = 0$, $p = 0.95$; Fig. 2C).

Ammonium uptake in Yellowstone Lake was comparable to $\text{NH}_4^+$ uptake in oligotrophic Flathead Lake, Montana (12.6 to 240 $\mu$g N m$^{-3}$ hr$^{-1}$; (Dodds et al. 1991). Pelagic microbes in Yellowstone Lake demanded less $\text{NH}_4^+$ than an eutrophic Alaskan Lake (140 to 51,700 $\mu$g N m$^{-3}$ hr$^{-1}$; (Gu and Alexander 1993), and eutrophic Lake Balaton, Hungary (110 to 1560 $\mu$g N m$^{-3}$ hr$^{-1}$; (Presing et al. 2001).

DISCUSSION

Zooplankton excretion supplied the majority of $\text{NH}_4^+$ demanded by phytoplankton in Yellowstone Lake; however, cutthroat trout excretion supplied a fraction of demand. In Yellowstone Lake, zooplankton excretion supplied 86% of the $\text{NH}_4^+$ demanded by phytoplankton currently (Tronstad 2008). Our model suggested that phytoplankton uptake was similar between 1976 and 2006, thus zooplankton would have supplied ~100% of the $\text{NH}_4^+$ demanded in the past. Cutthroat trout excretion supplied 0.23% of current demand. Assuming demand has not changed, cutthroat trout supplied 0.45% of past demand. Thus, comparing animal fluxes to nutrient demand is useful when estimating the importance of fluxes within the ecosystem.

The indirect effect of lake trout on phytoplankton was probably greater than their direct effect through changes in excretion fluxes. The introduction of lake trout facilitated a trophic cascade that lowered phytoplankton biomass (Tronstad 2008). Despite changes in excretion fluxes, native cutthroat trout excretion was a minor part of nutrient cycling in Yellowstone Lake. Our results were contrary to Gla hot and Vanni (2005) who reported that the direct effect of blue gill ($\text{Lepomis macrochoiris}$) excretion was greater than their indirect effect on phytoplankton. Phytoplankton biomass indirectly decreased by $\frac{1}{2}$ to $\frac{1}{6}$ after the introduction of lake trout resulting in 1.6 m deeper Secchi disk measurements in Yellowstone Lake (Tronstad 2008). Similar to other lakes (e.g., Winder and Schindler 2004), climate change increased water temperature by 0.29°C/decade in Yellowstone Lake. In our model, warmer water temperatures cancelled the effect of decreased phytoplankton biomass resulting in no change in modeled $\text{NH}_4^+$ uptake. If we used temperature or Secchi disk depth alone to predict changes in uptake, we would have predicted higher and lower uptake, respectively.

CONCLUSIONS

Climate change and invasive species can interact in surprising ways. Here, climate change and invasive species interacted additively resulting in no change in modeled $\text{NH}_4^+$ uptake.
Warmer water temperatures cancelled the effect of a sparser phytoplankton assemblage induced by invasive lake trout.

**LITERATURE CITED**


