

Introduced lake trout alter nitrogen cycling beyond Yellowstone Lake

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Abstract. Introduced predators can have large effects on the ecosystem in which they were introduced, but how much these effects extend to other ecosystems beyond the invaded one is less known. We compared how lake trout (*Salvelinus namaycush*) affected nutrient cycling in an invaded and adjacent ecosystem in Yellowstone National Park, Wyoming, USA. Introduced lake trout in Yellowstone Lake caused the native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) population to decline. Native cutthroat trout are a dominant animal in the lake and may alter nutrient cycling in both Yellowstone Lake where they reside and in tributary streams used for spawning. We estimated changes in nutrient transport and nutrient uptake in both Yellowstone Lake and Clear Creek, a spawning stream, before and after the invasion of lake trout. Annual area-specific excretion fluxes from cutthroat trout were nine times higher in Clear Creek compared to Yellowstone Lake when cutthroat trout were abundant. However, fluxes within the lake and stream were similar after cutthroat trout declined. In Yellowstone Lake, zooplankton excretion supplied 86% of ammonium (NH_4^+) that was taken up, but cutthroat trout only supplied <0.3% after the introduction of lake trout. Conversely, NH_4^+ excreted by cutthroat trout was likely a major flux in Clear Creek, because NH_4^+ fluxes from cutthroat trout exceeded watershed export of NH_4^+ in years when >3000 cutthroat trout spawned. Furthermore, NH_4^+ excretion fluxes from spawning cutthroat trout in Clear Creek supplied up to 6.1% of the NH_4^+ demanded by microbes after the introduction of lake trout. However, based on modeled past NH_4^+ uptake, we estimated that up to 60% of NH_4^+ excreted by spawning cutthroat trout may have been taken up by stream microbes when cutthroat trout were abundant. Therefore, transported NH_4^+ from spawning cutthroat trout was likely an integral part of N cycling in tributary streams in the past. By comparing the effects of declining cutthroat trout on two ecosystems, we show that lake trout had a larger effect on N cycling within an adjacent stream ecosystem than the invaded lake ecosystem itself, because the migratory behavior of cutthroat trout concentrated them in spawning streams increasing their effect.

Key words: benthic-pelagic coupling; diet; excretion; invasive species; nitrogen; nutrient cycling; nutrient transport; nutrient uptake; phosphorus; spawning; stream; Yellowstone cutthroat trout.

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INTRODUCTION

Introduced animals can alter the density,

community interaction, and ecosystem function of native species in the invaded habitat (Parker et al. 1999). Although most invasive animals have

little effect in the recipient ecosystem, some invaders can strongly alter ecosystem processes (Strayer 2012). Invasive animals may affect ecosystems via two mechanisms. First, dominant invasive animals can directly affect ecosystem processes via high biomass. For example, zebra mussels (*Dreissena polymorpha*) dominated the Hudson River rerouting resources from the pelagic zone and deep-water sediments to vegetated shallows and zebra mussel beds (Strayer et al. 1999). Invasive mud snails dominated nutrient cycling, shifting element flows away from native stream invertebrates (Hall et al. 2003). Second, introduced predators may cause cascading effects that indirectly alter ecosystem function. For example, introduced arctic foxes (*Alopex lagopus*) reduced the density of native seabirds on the Aleutian archipelago indirectly altering nutrient transport and plant community composition (Croll et al. 2005). Wolves recolonizing Banff National Park altered the community by consuming elk, which indirectly increased songbird populations (Hebblewhite et al. 2005).

If introduced predators can lower the population size of a dominant native animal, then this predator may have large indirect effects on an ecosystem. One pathway that may be disrupted is nutrient cycling. For example, animal excretion and egestion can supply a large proportion of the nutrients demanded by primary producers (Grimm 1988a,b, Vanni 2002, Hall et al. 2003, McIntyre et al. 2008). In lakes, adding a piscivorous fish reduced nutrient excretion by all fish in the ecosystem (Schindler et al. 1993). The predator may indirectly alter ecosystem processes via a trophic cascade that alters primary production (Carpenter et al. 2001). Introduced brown trout (*Salmo trutta*) reduced native *Galaxias* fish and induced a trophic cascade in invaded New Zealand streams that indirectly increased algal biomass and nitrogen uptake in riffles (Simon et al. 2004).

Ecosystem-level effects of invasive predators may extend beyond the habitat where they reside if native prey moves between ecosystems (Baxter et al. 2004, Epanchin et al. 2010, Sato et al. 2012). Affected ecosystems may extend beyond areas adjacent to invaded ecosystems and be hundreds of kilometers away depending on the behavior of the animals that connect them (Reiners and

Driese 2004), such as salmon (Holtgrieve and Schindler 2011). Despite an abundance of literature demonstrating that resources from one ecosystem can affect another, few subsidy studies have integrated an ecosystem-level approach (Marcarelli et al. 2011). Movement of animals can represent large nutrient fluxes between habitats, such as through regular or periodic movements (Meyer et al. 1983, Post et al. 1998, Gende et al. 2002). Invasive predators may disrupt the abundance, size or behavior of migrating native species, and subsequently alter the flow of energy, material, or information between ecosystems (e.g., Baxter et al. 2004).

Predaceous lake trout (*Salvelinus namaycush*) were introduced to Yellowstone Lake, Yellowstone National Park, Wyoming (Kaeding et al. 1996) during the mid-1980s (Munro et al. 2005). The Yellowstone Lake ecosystem is an ideal location to test the idea that an invasive predator may alter ecosystem processes beyond the invaded habitat, because few other perturbations exist besides the introduction of an apex predator, lake trout and because lake trout focus on one prey, the formerly dominant Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*). Lake trout may alter nutrient cycling in Yellowstone Lake and adjacent tributary streams by reducing the dominant, native cutthroat trout population. The cutthroat trout populations has fluctuated over the last century, but abundance declined by 60% since 1990 (Fig. 1; Koel et al. 2005). Cutthroat trout abundance was low from 1953 to 1961 because of egg-taking and liberal creel limits. The abundance of cutthroat trout increased after regulations changed (1964–1992), but these fish declined after the introduction of lake trout (2002–2006). Cutthroat trout live in Yellowstone Lake and spawn in tributary streams for a few weeks each summer. Within the lake, cutthroat trout may transport nutrients from the benthic to the pelagic zone resulting in enhanced primary production (Vander Zanden and Vadeboncoeur 2002, Vanni 2002). Although cutthroat trout return to the lake at the end of spawning, during the few weeks they spend in these tributary streams they likely excrete large quantities of nitrogen because spawning densities are high.

We estimated how the introduction of lake trout and subsequent decline of cutthroat trout

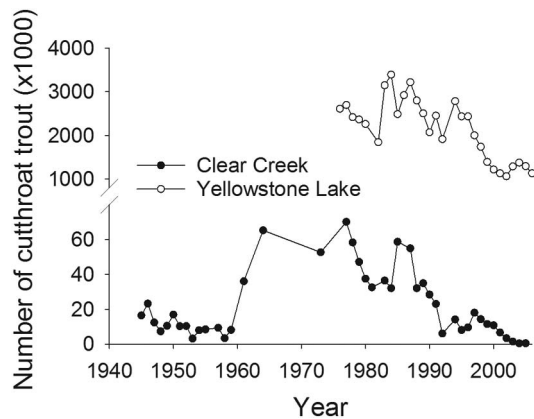


Fig. 1. Yellowstone cutthroat trout abundance varied through time. Spawning densities in Clear Creek were low in the 1940s and 1950s due to egg-taking and generous creel limits, but cutthroat trout recovered after regulations changed. Cutthroat trout abundance recently declined after the invasion of illegally introduced lake trout (~1985). The number of cutthroat trout was modified from Koel et al. (2005).

altered nutrient cycling in Yellowstone Lake and Clear Creek, a tributary stream. Specifically, we estimated to what degree nutrient transport and nutrient uptake changed within both ecosystems after the introduction of lake trout. We focused on nitrogen (N), because N limits primary producers in Yellowstone Lake (Interlandi and Kilham 1998). Although N cycling was not measured in Yellowstone Lake or tributary streams in the past when cutthroat trout were abundant, we modeled past excretion fluxes using cutthroat trout population estimates, measured excretion rates, and the area cutthroat trout occupied. Our objective was to estimate to what degree introduced lake trout changed processes within and beyond the invaded ecosystem of Yellowstone Lake.

METHODS

Study site

Yellowstone Lake and tributary streams in Yellowstone National Park, Wyoming, USA, are high elevation (>2350 m) ecosystems (Fig. 2). The region has a cold climate with long winters and short, cool summers. Yellowstone Lake is a mesotrophic (Kilham et al. 1996), dimictic lake that stratifies from mid-July to mid-September

and is ice covered from mid-December to late-May each year. Twenty-three percent of the lake surface area is <20-m deep (Benson 1961) and the mean depth of Yellowstone Lake is 43 m (Kaplinski 1991).

Yellowstone Lake holds the largest remaining population of native Yellowstone cutthroat trout (Fig. 3). Most adult cutthroat trout (>380 mm total length; TL) live in the littoral zone of Yellowstone Lake (<20 m depth). Mortality associated with spawning is 13–31% in streams (Gresswell 1995) and cutthroat trout may spawn several times during their life. After cutthroat trout fry emerge, they remain in streams from weeks to months before emigrating to Yellowstone Lake. In Yellowstone Lake, juvenile cutthroat trout (<380 mm TL) likely live in the pelagic zone until adulthood (Gresswell and Varley 1988).

Clear Creek, a tributary on the east side of the lake (Fig. 3), is one of 68 tributaries to Yellowstone Lake that historically had annual migrations of spawning cutthroat trout (Gresswell et al. 1997). Clear Creek is a 16-km, third order stream that drains 2.2% of the Yellowstone Lake watershed (Koel et al. 2006). Clear Creek has snow melt hydrology with the highest flows occurring in May and June, and the lowest flows in autumn. Stream water temperatures ranged between 0°C in January and a maximum of 18°C in summer (L. Tronstad, *unpublished data*). There are no resident fish in Clear Creek except for adult cutthroat trout that spawn from May to June each year (Koel et al. 2006) and juveniles that reside there during summer or through winter.

The native cutthroat trout population has drastically declined in Yellowstone Lake due to lake trout, whirling disease, and drought (Koel et al. 2005). Lake trout were illegally introduced into Yellowstone Lake around 1985 (Munro et al. 2005). Introduced lake trout were predicted to decrease the native cutthroat trout population (Stapp and Hayward 2002, Ruzycki et al. 2003), because the diet of these predators is primarily cutthroat trout (Ruzycki et al. 2003). Additionally, whirling disease, caused by the parasite *Myxobolus cerebralis*, was discovered in several spawning streams (Koel et al. 2006). In Yellowstone Lake, 6–16% of juvenile and adult cutthroat trout tested positive for *M. cerebralis* (Koel et al.



Fig. 2. Photo of Clear Creek flowing into Yellowstone Lake, Yellowstone National Park, Wyoming, USA.

2006). Finally, drought can affect juvenile cutthroat trout in small spawning streams by stranding individuals, and reducing egg and fry survival because of higher water temperatures. All three stressors likely reduced the cutthroat trout of Yellowstone Lake; however, lake trout predation probably had the greatest impact because whirling disease and drought are restricted to certain spawning streams, but the lake-wide cutthroat trout population has been affected by lake trout predation (Koel et al. 2005).

Excretion fluxes in Yellowstone Lake and Clear Creek

We measured the excretion flux of lake trout and cutthroat trout to estimate the degree to which these fish directly contributed to nutrient cycling in Yellowstone Lake and Clear Creek. We compared trout excretion fluxes to zooplankton excretion, microbial uptake, and watershed fluxes. We collected cutthroat trout from a fish weir at the outlet of Clear Creek and lake trout by gillnetting in Yellowstone Lake. We placed

individual fish in 20 L of water, and collected water samples at time zero and after 15 minutes to estimate the nutrient excretion rate of cutthroat trout ($n = 129$) and lake trout ($n = 47$). We used a short incubation time to minimize stress on cutthroat trout as outlined in our research permit from the National Park Service (NPS); however, we are aware that shorter incubation times may produce higher excretion rates compared to longer intervals (Whiles et al. 2009). We measured excretion of ammonium (NH_4^+) for all captured fish, and total dissolved nitrogen (TDN), total dissolved phosphorus (TDP) and dissolved organic nitrogen (DON) for 39 cutthroat trout (450–575 mm TL). We measured NH_4^+ (method detection limit (MDL) = $0.2 \mu\text{g NH}_4^+\text{-N/L}$) using a fluorometric assay (Taylor et al. 2007). We digested samples with persulfate (Koroleff 1983, Qualls 1989) to estimate TDN and TDP, and analyzed samples for nitrate (NO_3^-) and soluble reactive phosphorus (SRP) using automated colorimetry (Alpkem or Technicon; Institute of Ecology Stable Isotope Laboratory in

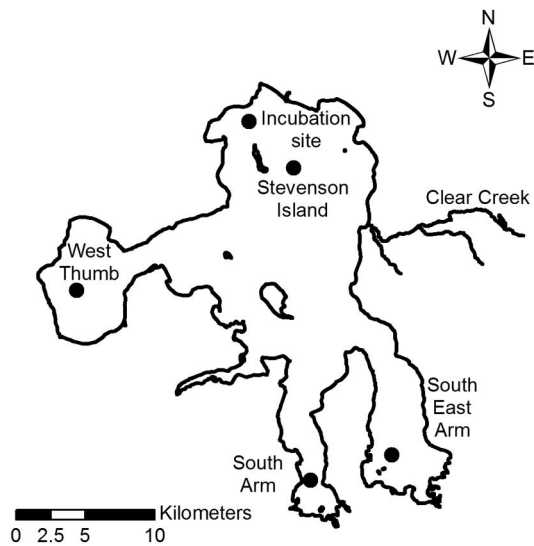


Fig. 3. Map of the Yellowstone Lake watershed showing the four sampling locations on Yellowstone Lake (east of Stevenson Island, South Arm, Southeast Arm and West Thumb). We incubated NH_4^+ uptake samples at depth in northern Yellowstone Lake. Clear Creek, one of ~68 tributary streams that cutthroat trout spawn in, flows into the east side of Yellowstone Lake.

Athens, Georgia, USA). Nitrate concentrations were measured using an ion chromatograph (Dionex ICS 2000 with an AS18 analytical column, Sunnyvale, California, USA; MDL = $0.76 \mu\text{g NO}_3^-/\text{L}$). We calculated DON by subtraction.

The relationship between fish body size and excretion rate could not be demonstrated, because all cutthroat trout were in a narrow length range (400–600 mm TL; 136–506 g dry mass; M). We could not sample smaller cutthroat trout; therefore, we measured NH_4^+ excretion rates of lake trout (200–570 mm TL; 12–405 g M) from Yellowstone Lake. We assumed that using another salmonid within the same ecosystem was the best alternative to form a size-dependent excretion model. We logged terms (base 10) and used ordinary least squares (OLS) regression (SPSS, version 12.0.1) to create a predictive allometric cutthroat trout and lake trout excretion model based on individual dry mass. The slope of our cutthroat trout and lake trout model (0.70 using reduced major axis linear regression for comparison only) was similar to other slopes

measured for Bonneville cutthroat trout (0.71; *Oncorhynchus clarkii utah*), kokanee salmon (0.96; *Oncorhynchus nerka*; Wheeler et al. 2014), rainbow trout (0.62; *Oncorhynchus mykiss*), brook trout (0.47; *Salvelinus fontinalis*; Paulson 1980, Sereda et al. 2008), and brown trout (0.75; *Salmo trutta*; Villéger et al. 2012). Reduced major axis linear regression allows biologically interpreting the slope parameter in a symmetric relationship (Warton et al. 2006) whereas our predictive allometric OLS model allowed us to estimate the excretion rate based on the trout mass. We did not calculate nutrient fluxes using a size-specific excretion model (except for NH_4^+) because the relationship between TDN, DON, TDP, and fish length were not significant, and we did not collect these data from lake trout.

We estimated the population size and length distribution of cutthroat trout to calculate the flux of nutrients from these fish in Yellowstone Lake. We used a population estimate, and annual indices of abundance and length to estimate the number of cutthroat trout in Yellowstone Lake through time (Koel et al. 2005, Tronstad et al. 2010). Ruzycki et al. (2003) estimated that 1.74 million (± 0.53 ; 95% confidence interval) cutthroat trout >100 mm total length (TL) lived in Yellowstone Lake in 1998 using hydroacoustics. The NPS and USFWS annually monitored the cutthroat trout population with standardized fall multi-mesh gillnetting surveys since 1976 (catch per unit effort (CPUE); cutthroat trout/net; Koel et al. 2005). We estimated that the cutthroat trout population was 1.37 times larger in 1979 (CPUE = 13.6 ± 1.3 cutthroat trout/net; 95% confidence interval) compared to 1998 (CPUE = 9.9 ± 1.3 cutthroat trout/net) using the CPUE index, and assuming a linear relationship between population size and CPUE.

Gillnets did not efficiently capture cutthroat trout <370 mm TL; therefore, we modeled the abundance of cutthroat trout in each 10 mm length class between 100 and 600 mm. We calculated the linear relationship between CPUE (cutthroat trout/net) in each length class >370 mm TL (CPUE_L) for each year (1976–1999) as $\text{CPUE}_L = mL + b$, where L is the length class (mm), m is a negative slope representing the change in CPUE between each length class, and b is the Y-intercept. The length-frequency data after 1999 indicated that the number of cutthroat trout

between ~320 and 430 mm TL was lower than previous years (the relationship between CPUE and length classes >370 mm TL was positive). Thus, we regressed cutthroat trout >440 mm TL against CPUE. Because CPUE of cutthroat trout between 370 and 430 mm TL after 1999 were lower than predicted, we used the collected (rather than estimated) number of cutthroat trout in these length classes to account for changes in the size distribution.

After modeling the CPUE of cutthroat trout in each length class, we estimated the proportion of the cutthroat trout population (CT_i) in each length class by

$$CT_i = \left(\frac{CPUE_L}{\sum CPUE} \right) \quad (1)$$

where $CPUE_L$ is calculated for each length class and $\sum CPUE$ is the total number of cutthroat trout caught summed across length classes. We calculated the number of cutthroat trout in each length class (Y_i) in Yellowstone Lake each year by multiplying the cutthroat trout population estimate by the proportion of fish in each length class.

In Yellowstone Lake, we calculated the flux of NH_4^+ excreted from cutthroat trout (F_L) by multiplying the excretion rate by the number of cutthroat trout in each length class and dividing by the affected volume of the lake epilimnion

$$F_L = \frac{\sum_{i=1}^l (a \times M_i^b) Y_i}{V} \quad (2)$$

where l is the number of length classes, F is the excretion flux from cutthroat trout ($\text{mg N m}^{-3} \text{ h}^{-1}$), M_i is individual cutthroat trout dry mass (g) for each length class, Y_i is the estimated number of cutthroat trout in each length class in Yellowstone Lake, a (0.30) and b (0.46) are constants based on our cutthroat trout and lake trout excretion model, and V is the volume (m^3) of the epilimnion. We calculated fluxes to 20 m depth, because most cutthroat trout live within 20 m of the water surface (Benson 1961) and the lake is stratified to ~20 m during summer stratification. We calculated NH_4^+ fluxes using the entire surface area of Yellowstone Lake (vs. the littoral zone), because the epilimnion is probably well mixed during summer stratification by afternoon

winds blowing across a ~22 km fetch. We multiplied the volumetric flux by 20 m depth to calculate areal fluxes ($\text{mg N m}^{-2} \text{ h}^{-1}$). To estimate fluxes of TDN, DON, and TDP, we used the same approach as for NH_4^+ (Eq. 2) except instead of the size-specific excretion model we used a mean excretion rate (E ; $\text{mg N or P fish}^{-1} \text{ h}^{-1}$), $F = EY/V$, where Y is the estimated total number of cutthroat trout in Yellowstone Lake. Cutthroat trout wet mass was calculated from TL using data from 19,213 cutthroat trout from Yellowstone Lake (Yellowstone National Park, unpublished data). Lake trout wet mass was estimated from TL using a published relationship predicting the 75th percentile of mass (Piccolo et al. 1993). Dry mass of salmonids was calculated as 22% of wet mass (Cyr and Peters 1996).

Cutthroat trout transport nutrients from benthic to pelagic habitats in Yellowstone Lake by consuming benthic invertebrates and excreting these nutrients in the open water of the epilimnion. Cutthroat trout also recycle nutrients in the open water by consuming zooplankton and excreting these nutrients in the open water. We multiplied the proportion of cutthroat trout diet from benthos by the total excretion flux to estimate the flux of benthic nutrients transported to the open water of Yellowstone Lake over time. We used data from past studies and collected diet samples from live-caught fish in our study to estimate the proportion of benthic invertebrates in cutthroat trout diet. In 1957 and 1958, Benson (1961) collected stomach contents of 344 and 429 cutthroat trout, respectively, between 150 and 400-mm TL from four areas of Yellowstone Lake between 15 July and 15 October. In 1970, Dean (1971) collected the stomach contents of 81 cutthroat trout in 4 areas of northern Yellowstone Lake using gillnets, electrofishing, and seines. Scott (1977) analyzed the diet of 56 cutthroat trout between 105 and 405 mm TL collected with a gill net near Stevenson Island in October 1974. In 1989, stomach contents of 132 cutthroat trout were collected from 11 areas of Yellowstone Lake during 11–15 September using gill nets (Jones et al. 1990). We collected stomach contents of 8 cutthroat trout caught using artificial flies in northern Yellowstone Lake in June 2005 by flushing stomachs using a syringe and plastic tubing. We identified diet items to the lowest level possible and measured length for biomass

estimates (Benke et al. 1999). We estimated the percent of benthic invertebrates (vs. zooplankton) in the diet of cutthroat trout based on biomass (1957, 1958, and 2004) or volume (1970 and 1989). We used OLS regression to estimate the relationship between the percent of cutthroat trout that ate amphipods and cladocerans, and the abundance of cutthroat trout (number of spawning cutthroat trout in Clear Creek; Data Desk 6.1, Data Descriptions, Ithaca, New York, USA). We used the number of spawning cutthroat trout in Clear Creek as a measure of cutthroat trout abundance, because spawning trout have been counted since 1945 and standardized gill netting in Yellowstone Lake did not begin until 1976. We multiplied the percent cutthroat trout diet from benthic invertebrates by the overall excretion rate to calculate the amount of excretion derived from benthic sources. We regressed benthic nutrients transported by the number of spawning cutthroat trout to estimate how much nutrient transport in Yellowstone Lake changed with cutthroat trout abundance.

In Clear Creek, we calculated NH_4^+ excretion fluxes from cutthroat trout (F_S ; $\mu\text{g N m}^{-2} \text{h}^{-1}$) by multiplying the number of cutthroat trout in stream each day (s) by the excretion rate (E ; $\mu\text{g N fish}^{-1} \text{h}^{-1}$), based on the average dry mass (M ; g) of spawning cutthroat trout each year, divided by the spawning area (d ; m^2), $F_S = E_S/d$. The number of spawning cutthroat trout moving upstream into Clear Creek was counted daily at a fish weir at the outlet of Clear Creek during the spawning season. We divided the annual number of cutthroat trout captured in the weir by the average length of the spawning season (65 days) and multiplied by the number of days a spawning cutthroat trout remains in stream (21 days; T. Koel, *unpublished data*) to calculate the number of trout in stream each day. Cutthroat trout swam farther upstream when more fish spawned. We visually surveyed the extent of spawning in Clear Creek (2004), and used past observations to estimate distance when larger numbers of cutthroat trout spawned (Jones et al. 1978) to estimate the upstream distance cutthroat trout swam. We regressed the number of spawning cutthroat trout (SCT) by distance spawned upstream (D ; 2900–9700 m; $D = 0.098 \times SCT + 2900$) and used a mean stream width of 5

m based on field measurements to calculate area (Jones et al. 1980). The mean length of spawning cutthroat trout was similar from 1952 to 1999 (390 ± 5 mm TL), but after 1999 length increased up to 505 mm TL in 2006 (Kaeding 2013). We used the same method as for NH_4^+ , except we used a mean excretion rate instead of the size-specific model to estimate excretion fluxes of TDN, DON, and TDP in Clear Creek.

We used regression analysis and parametric bootstrapping to estimate fluxes and associated error in measured cutthroat trout and lake trout excretion in Yellowstone Lake and Clear Creek. We calculated estimation error using bootstrapping (done in Microsoft Excel and Visual Basic) by randomly selecting 1000 values of CPUE and the cutthroat trout population assuming these estimates were normally distributed. To quantify error in the number of cutthroat trout per length class and size-specific excretion rate, the slope, x , and y variables were randomly chosen from normal distributions based on means and standard errors. We calculated the y -intercept for each relationship, because the slope and y -intercept are negatively correlated. Fluxes were calculated 1000 times per year according to the calculations for Yellowstone Lake and Clear Creek detailed above. We formed 95% confidence intervals as the 0.025 and 0.975 quantiles of the bootstrap distribution.

We measured zooplankton excretion rates by collecting zooplankton from Yellowstone Lake in August 2007. Between two and 11 individuals of the same genus were placed in 10 mL of deionized water at lake temperature and incubated for 70–130 minutes. Incubating zooplankton in deionized water may have stressed individuals, but our excretion estimates overlapped with those of Wen and Peters (1994). Initial and final water samples were collected and analyzed for NH_4^+ . We measured the length of each individual and estimated dry mass using published length-mass relationships (Dumont et al. 1975, Downing and Rigler 1984). We regressed $\log_{10}$ mean individual biomass (g M) against $\log_{10}$ excretion rate ($\text{mg N ind}^{-1} \text{h}^{-1}$) to calculate a linear size-specific excretion rate (SPSS, version 12.0.1). We used OLS regression because our goal was to predict excretion based on body size and not necessarily biologically interpret the slope parameter (Warton et al. 2006). We used data

from 2004 when we collected zooplankton during the ice-free season, and measured abundance and length on nine dates (Tronstad et al. 2010) to estimate the N excretion flux from the zooplankton assemblage. We multiplied our size-specific excretion rate by mean abundance for each species and size class on each sampling date. We multiplied zooplankton abundance from 1977 to 1980 by the size-specific excretion rate during the ice-free season (Tronstad et al. 2010) to calculate past zooplankton excretion. Zooplankton density and lengths were similar among years, thus we combined the 1977–1980 data to estimate their excretion. We plotted excretion against Julian day and we integrated the area under the curve to estimate total zooplankton excretion during the ice-free season of both periods. The mean daily excretion flux ($\mu\text{g N m}^{-2} \text{ d}^{-1}$) from zooplankton was calculated by dividing total excretion by the number of days in the period.

Comparing cutthroat trout excretion fluxes to NH_4^+ uptake in Yellowstone Lake

We compared excretion fluxes to current NH_4^+ uptake by phytoplankton to estimate the degree to which excretion fluxes from cutthroat trout and zooplankton contributed to nutrient cycling in Yellowstone Lake. We estimated phytoplankton NH_4^+ uptake by incubating $0.5 \mu\text{g N-}^{15}\text{NH}_4\text{Cl}$ in 2.5-L Nalgene polycarbonate bottles filled with lake water for 3 hours in early June, late July, and early October 2005; however, we did not estimate mineralization by phytoplankton. We collected water at 5, 10, and 15 m depths from 4 areas of Yellowstone Lake (two to three bottles per depth per site) and incubated bottles at their respective depths in northern Yellowstone Lake (Fig. 3). We kept water samples dark and on ice to minimize uptake during transportation to the laboratory after incubation. We collected phytoplankton by filtering 1.2 L of water through ashed 25-mm PALL type A/E glass fiber filters ($\sim 1\text{-}\mu\text{m}$ pore size) at three 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 ($t = 3 \text{ h}$). Filters were rinsed with 60 mL of deionized water after filtering samples to remove dissolved ^{15}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, Massachusetts, USA) interfaced with a Costech Analytical ECS4010 elemental analyzer (Valencia, California, USA) at the Colorado Plateau Stable Isotope Laboratory in Flagstaff, Arizona, USA.

We calculated the amount of ^{15}N taken up in each bottle as the fraction of excess ^{15}N in each sample ($^{15}\text{N}/\text{total N}$; atomic fraction; AF), $AF_{xs} = AF_{t=3\text{hr}} - AF_{t=0}$, where AF_{xs} is the AF excess, $AF_{t=3\text{hr}}$ is the AF after 3 hours of incubating, and $AF_{t=0}$ is the AF at time zero (sample taken immediately after ^{15}N was added). Total ^{15}N uptake flux ($^{15}\text{N}_{TU}$; $\mu\text{g N L}^{-1} \text{ h}^{-1}$) was calculated by

$$^{15}\text{N}_{TU} = \frac{N_{\text{filter}} AF_{xs}}{tv} \quad (3)$$

where N_{filter} is the mass of N on the filter (μg), t is the incubation time (h), and v is the volume of water filtered (L). Mean concentration of ^{15}N excess in the bottle ($\bar{C}_{^{15}\text{N}}$; $\mu\text{g } ^{15}\text{N/L}$) was calculated as

$$\bar{C}_{^{15}\text{N}} = \frac{0.2 + (0.2 - ^{15}\text{N}_{TU}t)}{2} \quad (4)$$

where $0.2 \mu\text{g } ^{15}\text{N/L}$ is the concentration added to each bottle. We used

$$k_p = \frac{^{15}\text{N}_{TU}}{\bar{C}_{^{15}\text{N}}} \quad (5)$$

to calculate the specific rate for an NH_4^+ molecule (k_p ; h^{-1}). We calculated phytoplankton NH_4^+ uptake flux (U_{phyto} ; $\mu\text{g N m}^{-3} \text{ h}^{-1}$) as $U_{\text{phyto}} = k_p C_A \times 1000$, where C_A is the ambient concentration of NH_4^+ ($\mu\text{g NH}_4^+\text{-N/L}$) in Yellowstone Lake water. We calculated the weighted average of the NH_4^+ uptake flux during the open water season by plotting uptake rate against Julian Day, and calculating the area under the curve.

Comparing cutthroat trout fluxes to other nutrient fluxes in Clear Creek

We calculated the nutrient flux from spawning cutthroat trout (g N or P/d) by multiplying excretion rate (g N or P fish $^{-1} \text{ d}^{-1}$; based on 15 minute incubations) by the number of fish in stream on an average day. We multiplied nutrient concentrations in water samples (g N or P/L) by discharge (L/d) on each date to calculate nutrient

export (g N or P/d) at the outlet of Clear Creek. We collected water samples at the outlet of Clear Creek at least weekly from May to July 2003.

We compared excretion fluxes to current NH_4^+ uptake to estimate the degree to which excretion fluxes from cutthroat trout contributed to nutrient cycling. We measured NH_4^+ uptake on 30 June 2004 and 30 June 2005 using stream spiraling methods (Newbold et al. 1981). We added NH_4^+ to the stream (stream concentrations increased to 17 $\mu\text{g N/L}$ in 2004 and 7, 10, and 18 $\mu\text{g N/L}$ in 2005) and measured the decline in NH_4^+ concentration downstream. By enriching stream water, we probably underestimated ambient NH_4^+ uptake because of lower efficiency of NH_4^+ uptake with increased concentrations (Mulholland et al. 2002). We collected water samples before and during nutrient additions at eight stations along 1.4 km of Clear Creek to estimate uptake. Bromide (Br^-) was added as a conservative tracer to correct for groundwater dilution and we measured NO_3^- to estimate nitrification. Bromide and NO_3^- concentrations were measured using an ion chromatograph (Dionex ICS 2000 with an AS18 analytical column; Sunnyvale, California, USA). We estimated the per meter uptake rate of NH_4^+ (k_1 ; m^{-1}) using discharge-corrected NH_4^+ concentrations at eight stations. We calculated uptake length (S_w ; m; average distance an NH_4^+ molecule travels downstream before being taken up by microbes), uptake velocity (V_f ; m/min ; corrected uptake length for stream depth and water velocity), and whole-stream NH_4^+ uptake flux (U ; $\text{mg N m}^{-2} \text{ min}^{-1}$) based on Newbold et al. (1981). We calculated the nutrient residence time (N_{RT} ; h) in Clear Creek as

$$N_{RT} = \frac{1}{vel \times k_1} \quad (6)$$

where vel is the mean water velocity (m/h). For 2005, we reported the average S , v_f , and U based on three enrichment concentrations in Clear Creek.

We estimated excretion as a function of the number of spawning trout relative to microbial demand through time to estimate the degree to which cutthroat trout altered nutrient cycling in tributary streams. The model does not predict total NH_4^+ uptake within Clear Creek, but rather the amount of cutthroat trout-derived NH_4^+

taken up by stream microbes. Therefore, when cutthroat trout were removed from the model, no net NH_4^+ uptake occurred in the stream, because we assumed the NH_4^+ mineralization rate was constant and equal to NH_4^+ uptake rate at the top of the stream reach (Brookshire et al. 2009). Demand through time varied only as a function of NH_4^+ concentration. We assumed that all variables were constant among years (e.g., climate, precipitation, temperature, etc.) except variables associated with cutthroat trout (i.e., number of spawning cutthroat trout, upstream spawning distance, NH_4^+ concentration as a function of cutthroat trout excretion, and the uptake efficiency (v_f) of cutthroat trout excretion changed as NH_4^+ concentration varied through time in Clear Creek). We modeled NH_4^+ uptake in Clear Creek by modifying the differential equation from Wollheim et al. (2001)

$$\frac{dH}{dx} = k_m H_0 + k_e A - k_1 H \quad (7)$$

where H is NH_4^+ flux (g N/min), x is distance downstream (m), k_m is NH_4^+ mineralization rate ($1/\text{m}$), H_0 is the flux of NH_4^+ at $x = 0$ (g N/min), k_e is fish excretion ($1/\text{min}$), A is the fish biomass distribution (g N/m), and k_1 is NH_4^+ uptake rate ($1/\text{m}$). We assumed that 11% of dry mass is equal to the mass of N in cutthroat trout (Griffiths 2006). We estimated NH_4^+ fluxes at 100-m intervals by solving the differential equation using the Euler method

$$H_{x+1} = H_x + (k_m H_0 + k_e A - k_1 H_x) \Delta x \quad (8)$$

where H_x and H_{x+1} are NH_4^+ fluxes (g N/min) at distance x and $x+1$ ($\Delta x = 100$ m reaches; Fig. 4). For the model, fish were evenly distributed throughout the stream. We calculated the areal flux of excretion retained ($\text{g N m}^{-2} \text{ h}^{-1}$) by dividing by the spawning area, which changed among years.

All variables in the stream uptake model were fixed among years, including mineralization, discharge ($2.25 \text{ m}^3/\text{s}$; historical mean from past reports), and the initial NH_4^+ concentration at $x = 0$ ($1.7 \mu\text{g N/L}$; mean concentration in Clear Creek in 2003), but cutthroat trout TL (mm) and the number of spawning cutthroat trout, based on historical data, changed among years. The NPS and USFWS recorded the number of spawning cutthroat trout since 1945. We calculated annual

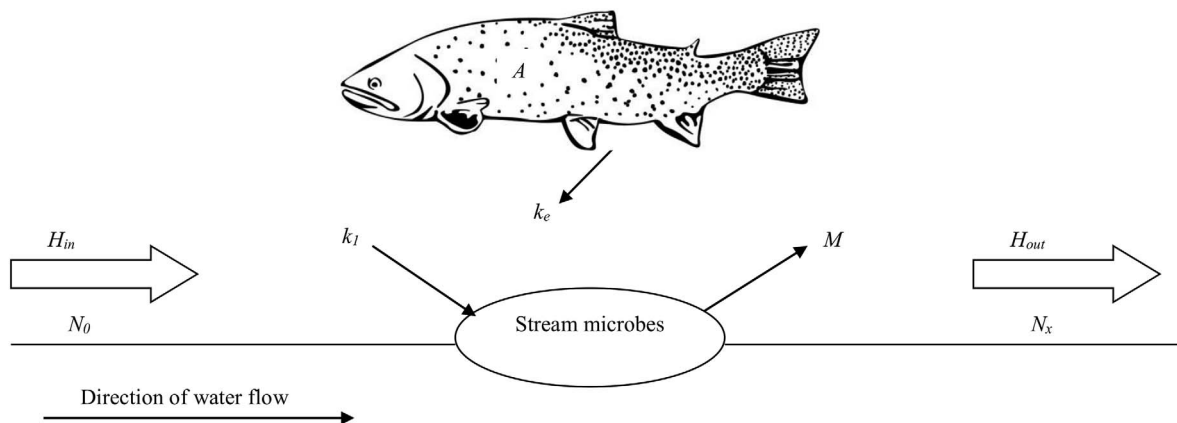


Fig. 4. Uptake of cutthroat trout excreted NH_4^+ in spawning streams based on a model modified from Wollheim et al. (2001). The biomass of spawning cutthroat trout (A ; g N/m) was distributed evenly throughout the stream and these fish excreted NH_4^+ (k_e ; min^{-1}). Stream microbes (e.g., bacteria and algae) took up excreted NH_4^+ from cutthroat trout (k_1 ; m^{-1}) and released mineralized NH_4^+ (k_m ; m^{-1}). In our model, we assumed $k_1 = M$ at the top of the reach. We calculated nitrogen fluxes at the top (N_0 ; g N/min) and bottom (N_x ; g N/min) of the reach, and estimated uptake of NH_4^+ excreted by cutthroat trout as the flux of NH_4^+ coming into the reach (H_{in} ; g N/min) plus total cutthroat trout excretion (g N/min) minus the flux of NH_4^+ leaving at the bottom of the stream reach (H_{out} ; g N/min). We assumed stream discharge was the same among years, but the number of spawning cutthroat trout, length of cutthroat trout, and distance spawned changed among years. See methods for more details. Line drawing by Christine Fisher.

error in excretion fluxes from cutthroat trout in Clear Creek based on error in measured excretion rates (excretion-based error). We ignored error in fish dry mass, because variance was minimal (mean CV = 0.95%). Uncertainty in spawning area and the number of spawning cutthroat trout was not included, because we lacked the necessary data for these calculations. The rate at which microbes assimilated NH_4^+ (k_1) may have been subject to altered NH_4^+ concentrations, because NH_4^+ demand (v_f) declines with stream NH_4^+ concentration (Dodds et al. 2002). Using data from Dodds et al. (2002) and Clear Creek in 2004 and 2005, we estimated the relationship between NH_4^+ demand and NH_4^+ concentration. We calculated NH_4^+ demand based on NH_4^+ concentration as a function of cutthroat trout density in each 100 m reach. We calculated total NH_4^+ from cutthroat trout retained by stream microbes in Clear Creek (N_R ; g N/min) as $N_R = H_{in} + (k_e A x) - H_{out}$, where H_{in} is the NH_4^+ flux from upstream (g N/min; constant), $k_e A x$ is total fish excretion (g N/min), and H_{out} is the NH_4^+ flux at the bottom of the reach (g N/min; Fig. 4). We calculated the percent of retained cutthroat trout excretion by

dividing N_R by $k_e A x$ and multiplying by 100.

RESULTS

Comparing cutthroat trout excretion fluxes in Yellowstone Lake and Clear Creek

Cutthroat trout excreted NH_4^+ , NO_3^- , DON, and SRP. Individual cutthroat trout and lake trout NH_4^+ excretion fluxes (E ; $\text{mg NH}_4^+\text{-N fish}^{-1} \text{ h}^{-1}$) increased with dry mass (Fig. 5). Cutthroat trout and lake trout dry mass (M ; g) related to NH_4^+ excretion rates, $\log_{10} E = 0.46 \times \log_{10} M - 0.52$ ($t = 11.4$, $\text{df} = 174$, $r^2 = 0.43$, $P < 0.0001$; 95% confidence interval of slope = ± 0.08 and y -intercept = ± 0.18) or $E = 0.30 \times M^{0.46}$. Cutthroat trout (mean length was 511 mm TL and dry mass was 270 g) excreted $9.6 \pm 2.2 \text{ mg TDN-N fish}^{-1} \text{ h}^{-1}$, $3.8 \pm 1.3 \text{ mg DON-N fish}^{-1} \text{ h}^{-1}$, and $0.9 \pm 0.3 \text{ mg TDP-P fish}^{-1} \text{ h}^{-1}$. The molar N:P ratio of excreta was 47. Dissolved organic nitrogen and NH_4^+ were excreted in nearly equal proportions.

Cutthroat trout excretion fluxes decreased in Clear Creek and Yellowstone Lake as the number of cutthroat trout declined. In 2003, stream NH_4^+ concentrations doubled when 3432 cutthroat trout spawned, but stream concentrations were

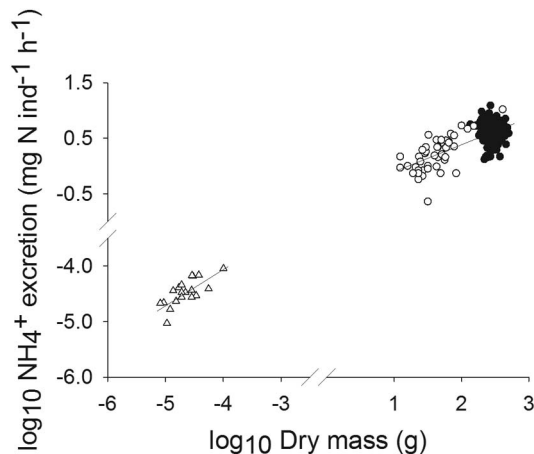


Fig. 5. Salmonid individual dry mass (M ; g) explained 43% of the variation in salmonid NH_4^+ excretion ($\log_{10}E = 0.46 \times \log_{10}M - 0.52$; where E is $\text{mg N ind}^{-1} \text{ h}^{-1}$). Zooplankton individual dry mass explained 55% of the variation in NH_4^+ excretion ($\log_{10}E = 0.64 \times \log_{10}DM - 1.47$).

still low (Fig. 6). However, calculated excretion fluxes were over six times higher when cutthroat trout abundance was high (44,000 spawning cutthroat trout annually; 1964–1992) compared to after these fish declined (2,500 spawning cutthroat trout in 2002–2006; Table 1). Conversely, excretion fluxes in Yellowstone Lake decreased to a smaller degree as the cutthroat trout population declined. Calculated NH_4^+ fluxes from cutthroat trout in Yellowstone Lake were highest between 1976 and 1992 ($22 \pm 1.8 \mu\text{g N m}^{-2} \text{ h}^{-1}$; $1.1 \pm 0.52 \mu\text{g N m}^{-3} \text{ h}^{-1}$) when cutthroat trout were abundant (Fig. 1). However, excretion fluxes decreased to $9 \mu\text{g N m}^{-2} \text{ h}^{-1}$ ($0.47 \mu\text{g N m}^{-3} \text{ h}^{-1}$; Table 1) after cutthroat trout declined in 2006. Therefore, cutthroat trout annually excreted ~ 2.3 times more nutrients in Yellowstone Lake in 1976–1992 compared to 2006 (Table 1).

Both instantaneous and annual estimates suggest that the change in nutrient excretion by cutthroat trout was far greater in Clear Creek compared to Yellowstone Lake. The calculated instantaneous flux ($\mu\text{g N}$ or $\text{P m}^{-2} \text{ h}^{-1}$) of nutrients suggested that cutthroat trout excreted ~ 50 times more nutrients per m^2 (NH_4^+ , TDN, DON, and TDP) in Clear Creek compared to Yellowstone Lake when cutthroat trout were

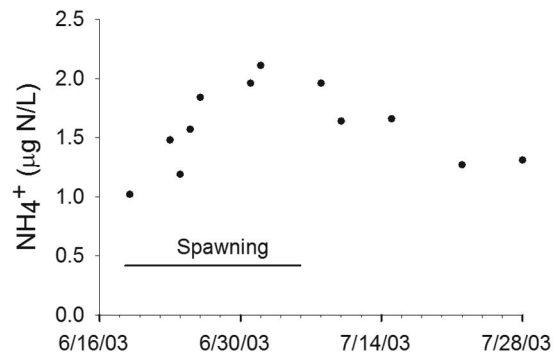


Fig. 6. Ammonium concentrations ($\mu\text{g N/L}$) doubled at the outlet of Clear Creek when 3432 cutthroat trout spawned during 2003. The bar indicated when cutthroat trout were spawning in Clear Creek.

abundant, but fluxes decreased thereafter. Cutthroat trout excreted two times more NH_4^+ in Yellowstone Lake and over six times more NH_4^+ in Clear Creek compared to post-lake trout invasion (Table 1). Cutthroat trout spend ~ 65 days each year in Clear Creek, and live in Yellowstone Lake the rest of the year. We calculated annual nutrient fluxes in both ecosystems to account for these differences. When cutthroat trout were abundant (1964–1992), these fish excreted ~ 8.5 times more nutrients per m^2 in Clear Creek than in Yellowstone Lake annually (Table 1; Fig. 7A). After cutthroat trout abundance declined (2005 and 2006), they annually excreted similar fluxes of NH_4^+ in Clear Creek and Yellowstone Lake. Annual estimates suggested that the decline of cutthroat trout lowered nutrient fluxes to a larger degree in adjacent spawning streams than in Yellowstone Lake, because spawning streams are smaller (higher density of cutthroat trout in spawning streams than Yellowstone Lake) and cutthroat trout swam farther upstream in the past.

Because of changes in diet of native trout, the amount of benthic nutrients transported to the open water of Yellowstone Lake did not change with cutthroat trout abundance ($t = -0.115$, $P = 0.92$, $r^2 = 0.004$, $df = 3$). The proportion of cutthroat trout diet derived from benthic invertebrates varied with native trout abundance. More cutthroat trout consumed amphipods (*Hyalella* and *Gammarus*) when their abundance was low (Fig. 8A), $a = -0.000616(\pm 0.000395) \times \text{SCT} + 45.4(\pm 13.3)$ ($t = -3.06$, $P = 0.038$, $r^2 = 0.70$,

Table 1. Yellowstone cutthroat trout excrete nutrients in the open water of Yellowstone Lake and lake nutrients in spawning streams (e.g., Clear Creek). Excretion fluxes of ammonium (NH_4^+), total dissolved nitrogen (TDN), dissolved organic nitrogen (DON), and total dissolved phosphorus (TDP) from cutthroat trout in Yellowstone Lake were lower than to Clear Creek on an hourly basis ($\mu\text{g N or P m}^{-2} \text{ h}^{-1}$) and when annual fluxes were adjusted for the time spent in each ecosystem ($\text{mg N or P m}^{-2} \text{ yr}^{-1}$).

Location and time period	NH_4^+	TDN	DON	TDP
A) $\mu\text{g N or P m}^{-2} \text{ h}^{-1}$				
Clear Creek				
1953–1961	332 ± 83	1230 ± 310	487 ± 123	115 ± 29
1964–1992	1040 ± 60	3710 ± 245	1470 ± 97	348 ± 23
2002–2006	162 ± 132	465 ± 401	184 ± 159	44 ± 38
Yellowstone Lake				
1976–1992	22 ± 1.8	72 ± 6.2	29 ± 2.5	7 ± 0.6
2002–2006	10 ± 1.0	35 ± 3.2	14 ± 1.3	3 ± 0.3
B) $\text{mg N or P m}^{-2} \text{ yr}^{-1}$				
Clear Creek				
1953–1961	518 ± 130	1920 ± 484	759 ± 192	180 ± 45
1964–1992	1620 ± 93	5790 ± 383	2300 ± 151	543 ± 36
2002–2006	253 ± 205	725 ± 625	287 ± 248	68 ± 59
Yellowstone Lake				
1976–1992	189 ± 16	634 ± 54	251 ± 21	59 ± 5
2002–2006	90 ± 8	303 ± 28	120 ± 11	28 ± 3

Notes: Cutthroat trout abundance was low from 1953 to 1961, because of egg-taking and liberal creel limits. The abundance of cutthroat trout increased after regulations changed (1964–1992), but these fish declined after the introduction of lake trout (2002–2006). Errors are 95% confidence intervals based on mean annual estimates.

$\text{df} = 4$, where a is the percent of cutthroat trout consuming amphipods and SCT is the number of spawning cutthroat trout in Clear Creek; Fig. 8B). Conversely, when cutthroat trout were abundant they consumed more zooplankton, $\text{zoo} = 0.00084 (\pm 0.00106) \times SCT + 30.1 (\pm 36.1)$ ($t = 1.55$, $P = 0.197$, $r^2 = 0.37$, $\text{df} = 4$ where zoo is the percent of cutthroat trout consuming cladocerans; Fig. 8C). Therefore, the percent of cutthroat trout diet from benthic invertebrates varied between 21 and 87% (based on biomass or volume) from 1957–2004 in Yellowstone Lake (Fig. 8D).

Comparing excretion fluxes from cutthroat trout to other nutrient fluxes in Yellowstone Lake

Ammonium fluxes from cutthroat trout were $<1\%$ of zooplankton excretion fluxes in the lake (Fig. 9A). Log zooplankton dry mass (M ; g) explained 55% of the variation in log NH_4^+ excretion flux (E ; $\text{mg N ind}^{-1} \text{ h}^{-1}$), $\log_{10} E = 0.64 \times \log_{10} M - 1.47$ ($t = 4.52$, $\text{df} = 17$; 95% confidence interval of slope = ± 0.28 and y -intercept = ± 1.30 ; Fig. 5). Although zooplankton stored 1.2 to 3 times more N than cutthroat trout in Yellowstone Lake, zooplankton excreted >200 times more NH_4^+ than did these fish (Fig. 9A), because zooplankton turned N over much faster (<2 days) than cutthroat trout (250 days).

Ammonium demand by phytoplankton varied

throughout the summer. Phytoplankton assimilated more NH_4^+ in July ($8.1 \pm 1.9 \text{ mg N m}^{-2} \text{ h}^{-1}$; $405 \pm 93 \mu\text{g N m}^{-3} \text{ h}^{-1}$), than June ($1.6 \pm 0.7 \text{ mg N m}^{-2} \text{ h}^{-1}$; $81 \pm 34 \mu\text{g N m}^{-3} \text{ h}^{-1}$) or October ($1.6 \pm 0.29 \text{ mg N m}^{-2} \text{ h}^{-1}$; $82 \pm 15 \mu\text{g N m}^{-3} \text{ h}^{-1}$; Tukey's: $P < 0.05$) in 2005. Ammonium residence time in Yellowstone Lake was shortest in June ($9.7 \pm 3.9 \text{ h}$) and July ($3 \pm 0.6 \text{ h}$), and longest in October ($38 \pm 5.8 \text{ h}$; Tukey's: $P < 0.05$).

Phytoplankton demanded far more NH_4^+ than that supplied by cutthroat trout in Yellowstone Lake, but about the same amount as zooplankton excretion fluxes. In 2005, cutthroat trout excreted $<0.3\%$ of the NH_4^+ demanded by phytoplankton, but zooplankton excreted 86% of the NH_4^+ demanded by phytoplankton in Yellowstone Lake (Fig. 9A). Atmospheric deposition of NH_4^+ did not account for changes in demand as the amount deposited near Yellowstone Lake was similar in the past and present ($\sim 9 \mu\text{g N m}^{-2} \text{ h}^{-1}$; <http://nadp.sws.uiuc.edu/>) and the flux was small (Fig. 9).

Comparing excretion fluxes from cutthroat trout to other nutrient fluxes in Clear Creek

Excreted nutrients from cutthroat trout were a large fraction of the NH_4^+ exported in Clear Creek, but a small fraction of total N export. Ammonium export from the Clear Creek water-

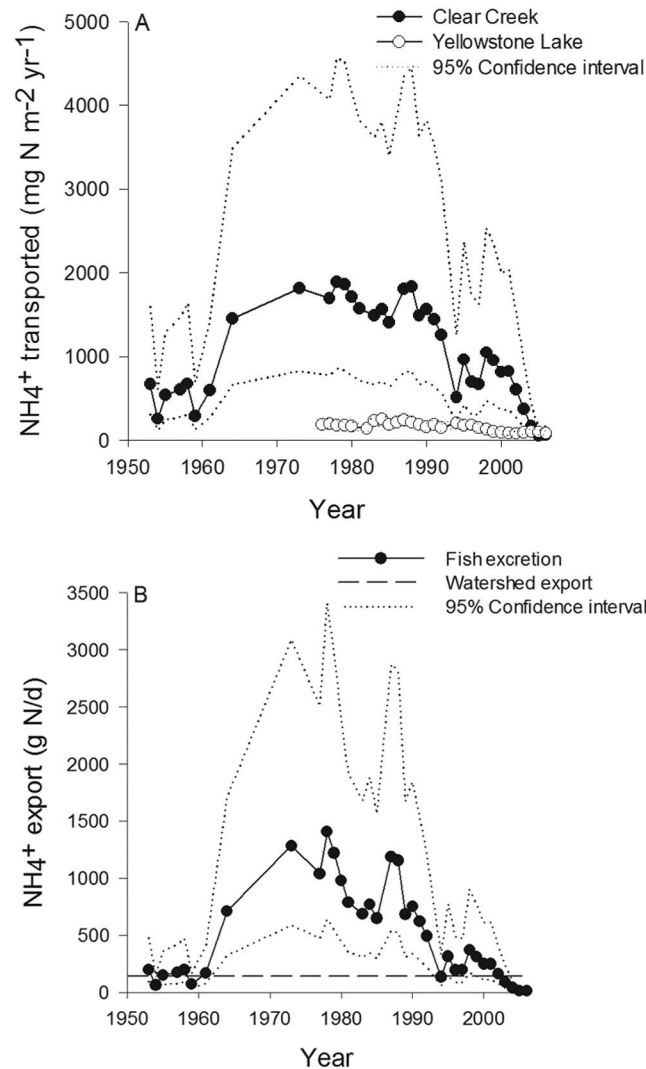


Fig. 7. (A) Estimated annual NH₄⁺ excretion fluxes from cutthroat trout (mg N m⁻² yr⁻¹) transported in Yellowstone Lake (1976–2006) and to Clear Creek (1953–2006, a tributary spawning stream) were lower than predicted in the past. Nutrient fluxes were 9 times higher in Clear Creek compared to Yellowstone Lake when cutthroat trout were abundant, but fluxes in these two ecosystems were similar after the decline of these fish. In Clear Creek, 95% confidence intervals are excretion-based error. In Yellowstone Lake, 95% confidence intervals are bootstrapped estimates. (B) Estimated NH₄⁺ excretion by cutthroat trout (g N/d) during spawning exceeded NH₄⁺ export (g N/d) in Clear Creek during years when >3000 cutthroat trout spawned. Ninety-five percent confidence intervals are excretion-based error.

shed averaged 211 g N/d (± 73 ; 95% CI) during summer 2003. Assuming export was similar among years, NH₄⁺ fluxes from cutthroat trout exceeded watershed export of NH₄⁺ in years when >3000 cutthroat trout spawned (Fig. 7B). Excreted NH₄⁺ from spawning cutthroat trout in the 1970s was likely over 6 times higher than

ambient NH₄⁺ export from Clear Creek. Conversely, cutthroat trout excretion was only a fraction of watershed sources of TDN (23%), DON (9.6%), and TDP (37%) in the past (1964–1992), and in the present (1% of TDN, 0.5% of DON, and 2% of TDP; Table 2).

Ammonium fluxes from cutthroat trout sup-

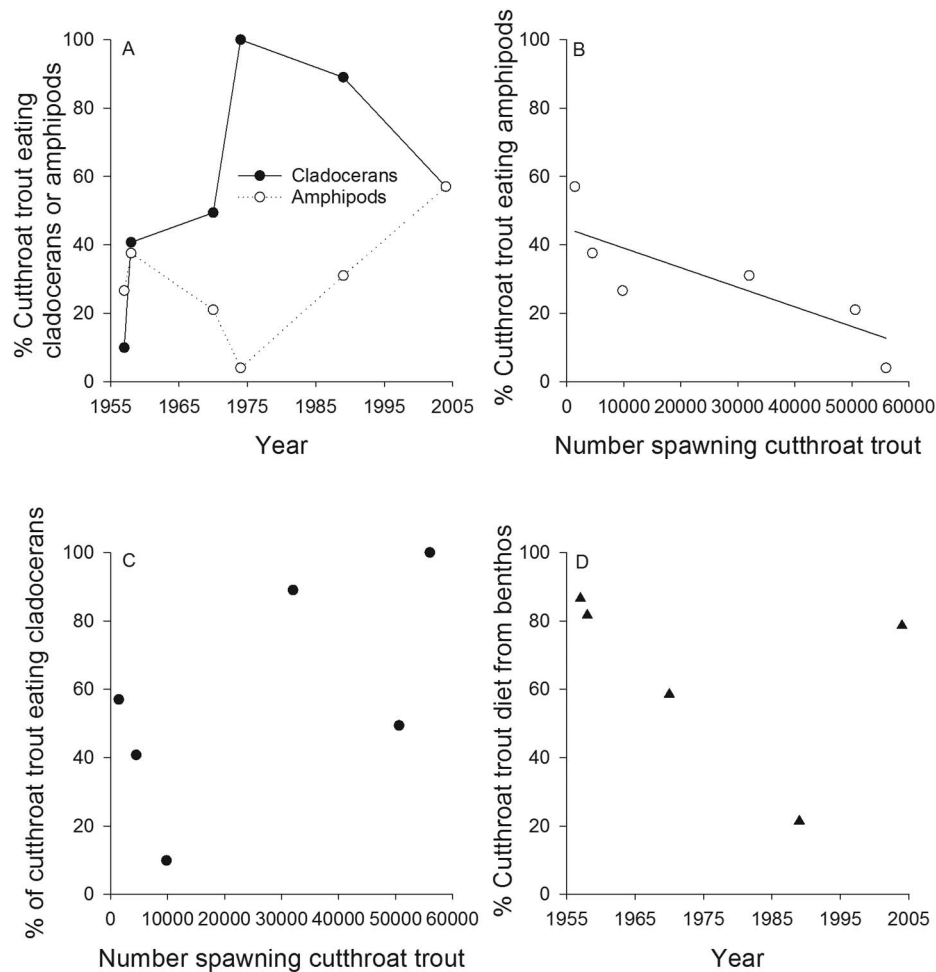


Fig. 8. (A) The diet of cutthroat trout in Yellowstone Lake varied through time. Cutthroat trout consumed more cladocerans and fewer amphipods when cutthroat trout were abundant (1970s and 1980s). (B) The percent of cutthroat trout eating amphipods decreased as cutthroat trout abundance increased ($a = -0.000616 \times SCT + 45.4$, $P = 0.038$; where a is the percent of cutthroat trout consuming amphipods and SCT is the number of spawning cutthroat trout in Clear Creek). (C) A higher percent of cutthroat trout consumed cladocerans when these fish were more abundant ($zoo = 0.00084 \times SCT + 30.1$, $P = 0.197$; where zoo is the percent of cutthroat trout consuming zooplankton and SCT is the number of spawning cutthroat trout in Clear Creek). (D) The percent of cutthroat trout diet from benthos was highest in the 1950s and 2004 when cutthroat trout were less abundant.

plied between 5.1 and 6.1% of the NH_4^+ demanded by microbes in Clear Creek in 2004 and 2005 (Fig. 9B). Excretion from cutthroat trout supplied $108 \mu\text{g N m}^{-2} \text{h}^{-1}$ in 2004 and $36 \mu\text{g N m}^{-2} \text{h}^{-1}$ in 2005. On the other hand, stream microbes assimilated $1770 \mu\text{g N m}^{-2} \text{h}^{-1}$ in 2004 and $703 \mu\text{g N m}^{-2} \text{h}^{-1}$ in 2005. As a result of higher microbial uptake in 2004, uptake length was shorter in 2004 (1250 vs. 2450 m), and v_f (8.7 vs. 3.9 mm/min) and U were higher in 2004,

indicating that NH_4^+ demand was higher in 2004 than 2005. Uptake lengths were 43–84% of the minimum upstream distance that cutthroat trout spawned.

We did not observe a change in NO_3^- concentrations when we increased in-stream NH_4^+ concentrations during either year. Conditions in Clear Creek were similar between 2004 and 2005 when we measured nutrient uptake except for NO_3^- concentrations and the number

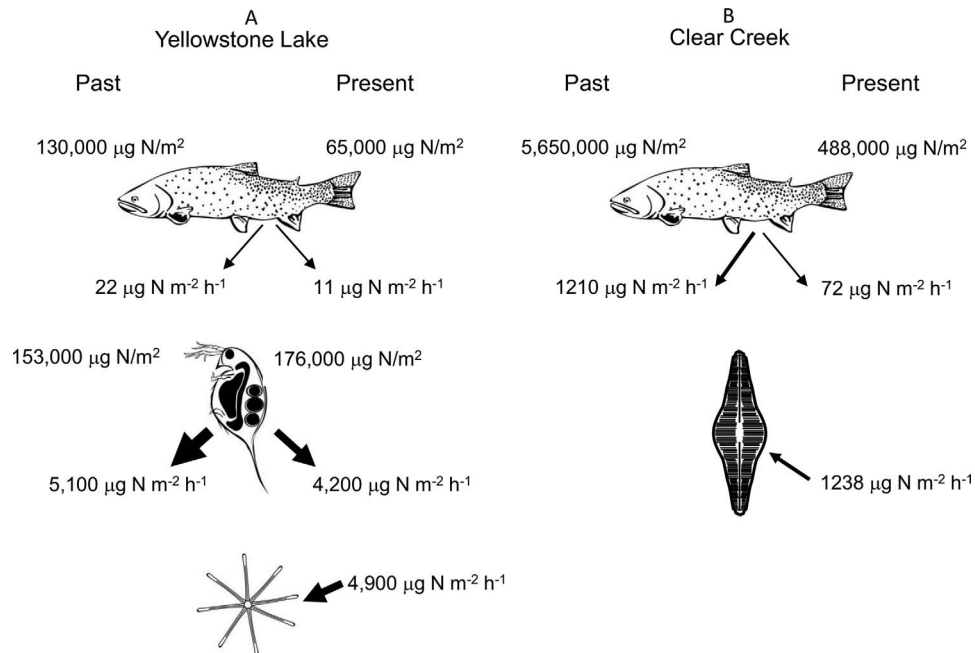


Fig. 9. (A) Estimated stocks and flows of epilimnetic nitrogen showed low direct effects of cutthroat trout decline. Zooplankton and cutthroat trout excretion ($\mu\text{g N m}^{-2} \text{h}^{-1}$) were lower after the introduction of lake trout. Excretion fluxes from cutthroat trout supplied $<0.3\%$ of the NH_4^+ demanded by phytoplankton, but zooplankton excretion fluxes supplied 86–100% of the NH_4^+ demanded by phytoplankton. (B) Estimated trout-derived stocks and flows of nitrogen in Clear Creek. Cutthroat trout biomass ($\mu\text{g N/m}^2$) and excretion ($\mu\text{g N m}^{-2} \text{h}^{-1}$) in Clear Creek were lower after the introduction of lake trout in Yellowstone Lake. Line drawings by Christine Fisher.

of spawning cutthroat trout. Ambient NH_4^+ concentrations ($3.2 \pm 0.2 \mu\text{g N/L}$), discharge ($1.5 \text{ m}^3/\text{s}$), water temperature ($10.5 \pm 1.5^\circ\text{C}$), and chlorophyll concentrations ($7.4 \pm 3.8 \mu\text{g/L}$) were similar in 2004 and 2005 during the experiments in Clear Creek, but wildfire increased ambient NO_3^- concentrations in 2005 ($100 \pm 10 \mu\text{g N/L}$) compared to 2004 ($3.7 \pm 1.2 \mu\text{g N/L}$; L. Tronstad, *unpublished data*), and the number of spawning

cutthroat trout was over three times higher in 2004 (1438 cutthroat trout) than 2005 (427 cutthroat trout).

We modeled microbial uptake of cutthroat trout excreted NH_4^+ through time to estimate the extent to which NH_4^+ fluxes from cutthroat trout contributed to nutrient cycling in the past. Ammonium demand (v_f ; mm/min ; comparable among streams by correcting for stream velocity

Table 2. Export of total dissolved nitrogen (TDN), dissolved organic nitrogen (DON), and total dissolved phosphorus (TDP; g N or P/d), measured at the outlet of Clear Creek, were higher than cutthroat trout excretion during spawning.

Measure	TDN	DON	TDP
Clear Creek export			
2003	14,200 $\pm$ 6870	13,500 $\pm$ 5900	816 $\pm$ 654
Cutthroat trout excretion			
1964–1992	3260 $\pm$ 525	1290 $\pm$ 208	305 $\pm$ 49
2002–2006	184 $\pm$ 171	73 $\pm$ 68	17 $\pm$ 16

Notes: Cutthroat trout excretion was calculated when these fish were abundant (1964–1992) and after cutthroat trout abundance declined (2002–2006). Errors are 95% confidence intervals based on mean annual estimates.

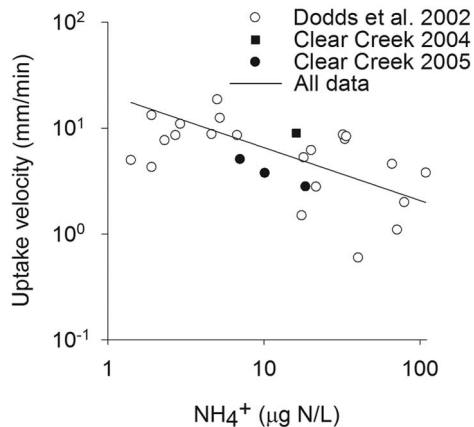


Fig. 10. Relationship between uptake velocity (v_f , mm/min) and NH_4^+ concentration ($\mu\text{g N/L}$) used to parameterize our stream model of nitrogen cycling.

and depth) in Clear Creek in 2004 and 2005, and 12 streams measured by Dodds et al. (2002) declined as NH_4^+ concentration ($\mu\text{g N/L}$) increased ($t = -5.56$, $r^2 = 0.56$, $df = 24$, $P < 0.0001$; Fig. 10), $\ln V_f = -0.50(\pm 0.18) \times \ln \text{NH}_4^+ + 3.03(\pm 0.49)$. Based on our assumptions, NH_4^+ uptake efficiency of cutthroat trout excreted NH_4^+ declined at higher concentrations of NH_4^+ . Despite lower uptake efficiency at higher NH_4^+ concentrations, the model suggested that stream microbes removed 10 times more cutthroat trout-excreted NH_4^+ in 1964–1992 compared to 2002–2006 (Fig. 11). According to the model, the most NH_4^+ from spawning cutthroat trout was taken up in 1978 ($716 \mu\text{g N m}^{-2} \text{h}^{-1}$) when 70,105 cutthroat trout spawned and the least was in 2005 ($11.4 \mu\text{g N m}^{-2} \text{h}^{-1}$) when 427 cutthroat trout spawned. Despite the decrease in uptake efficiency, the percent of excretion retained (32–60%) was nearly twice as high in 1964–1992 compared to 2002–2006 based on model predictions.

DISCUSSION

The introduction of lake trout and subsequent decline of cutthroat trout had a larger effect on nutrient cycling in an adjacent spawning stream, and likely other spawning streams, than in Yellowstone Lake itself. Cutthroat trout likely supplied a large flux of nutrients to Clear Creek prior to the invasion of lake trout; our model and

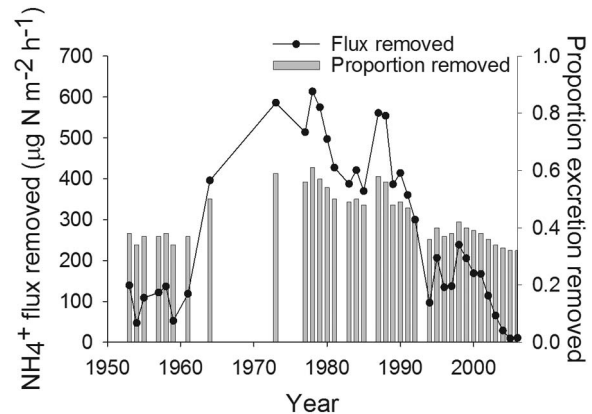


Fig. 11. The modeled flux of cutthroat trout NH_4^+ retained by stream microbes ($\mu\text{g N m}^{-2} \text{h}^{-1}$) was highest when cutthroat trout were abundant (1970s–1980s) and lowest after these spawning runs declined (2002–2006). The proportion of cutthroat trout-derived NH_4^+ retained by stream microbes was highest when cutthroat trout were abundant and declined in recent years.

estimates of other fluxes suggested that excretion fluxes from cutthroat trout were a substantial source of NH_4^+ for stream microbes when cutthroat trout were abundant. Conversely, excretion fluxes from cutthroat trout in Yellowstone Lake were likely small relative to demand before and after the invasion of lake trout. Ammonium fluxes from cutthroat trout were small relative to phytoplankton uptake and zooplankton excretion in Yellowstone Lake. Therefore, the uncertainty in modeled cutthroat trout densities probably had minimal effects on our conclusions, because the flux was so small.

The mechanism that changed N cycling in Yellowstone Lake differed from that in Clear Creek. In Clear Creek, the decline of cutthroat trout directly decreased excretion fluxes during spawning. Cutthroat trout densities were higher in spawning streams resulting in large fluxes of N in a relatively small area. However, cutthroat trout in Yellowstone Lake likely altered N cycling indirectly (Vanni 2002) through a trophic cascade ultimately reducing phytoplankton biomass (Tronstad et al. 2010). Densities of cutthroat trout were much lower and the volume of water was much larger in Yellowstone Lake, diluting excretion fluxes and thus direct effects on N-cycling from these fish relative to spawning

streams.

The indirect effects of invasive animals are probably not limited to the invaded habitat in many ecosystems. We showed that invasive lake trout had a greater effect on an adjacent tributary stream than in Yellowstone Lake where they live. Invasive animals may change function in many ecosystems when an invasive animal interacts strongly with native animals that move between ecosystems. For example, fewer aquatic insects emerged from alpine lakes stocked with trout in California lowering Rosy-Finch (*Leucosticte tephrocotis dawsoni*) abundance (Epanchin et al. 2010). Invasive animals may indirectly alter function in other ecosystems when animals in a food web strongly interact with the invader. For example, Baxter et al. (2004) demonstrated that invasive rainbow trout (*Oncorhynchus mykiss*) caused native Dolly Varden charr (*Salvelinus malma*) to feed on benthic invertebrates. Because of the altered feeding, fewer invertebrates emerged from the stream and were available to terrestrial spiders. Therefore, the indirect effects of many invasive species may affect adjacent ecosystems.

Invasive lake trout disrupted excretion fluxes from native cutthroat trout

Invasive animals can directly alter ecosystem processes (Strayer et al. 1999, Lovett et al. 2002, Hall et al. 2003, Simon et al. 2004). Despite an altered trophic structure in Yellowstone Lake (Tronstad et al. 2010), excretion fluxes from cutthroat trout were small under three (0.45% of animal excretion) and four trophic levels (0.23% of animal excretion). Trophic cascades can cause large changes in fish-derived nutrient fluxes. For example, fish excretion in a planktivore-dominated lake supported 30% of primary production, but fish excretion in a piscivore-dominated lake only supported 6–14% of primary production in a lake in Ontario, Canada (Findlay et al. 2005). Similarly, Schindler et al. (1993) calculated that fish excreted ~90% of P in a planktivore-dominated lake and ~20% of P in a piscivore-dominated lake in Michigan, USA (~80% by invertebrates).

The degree to which fish contributed to lake nutrient cycling can vary widely across ecosystems. In Yellowstone Lake, cutthroat trout contributed little N to phytoplankton demand before and after the introduction of lake trout.

Similarly, fish excretion supplied 3–10% of P demanded by microbes in an alpine lake (Sarnelle and Knapp 2005). Others concluded that fish were sinks of nutrients (Griffiths 2006, Sereda et al. 2007). However, fish can sometimes supply most nutrients demanded by microbes. For example, fish contributed 80% of P demanded by microbes in a Norwegian lake during summer (Brabrand et al. 1990) and gizzard shad excretion exceeded demand by phytoplankton in productive reservoirs (Vanni et al. 2006). Still, others suggested that all animal fluxes were small compared to mineralization by pelagic microbes in lakes (Hudson et al. 1999). Some of the variation in animal-derived fluxes in lakes may be explained by fish size, because body size regulates the amount of nutrients excreted by an individual. Smaller fish excrete at a higher mass-specific rate (Hall et al. 2007); therefore, mineralizing more nutrients in the water column. Most planktivores in other studies were smaller bodied minnows (e.g., Carpenter et al. 2001) that appeared to contribute more to nutrient cycling than did the much larger cutthroat trout in Yellowstone Lake.

The indirect effects of introduced lake trout on Yellowstone Lake caused larger changes in N cycling than the direct effects on cutthroat trout alone. In Yellowstone Lake, introducing lake trout altered feeding by cutthroat trout changing the structure of the zooplankton assemblage (Tronstad et al. 2010). Lowered feeding by cutthroat trout increased zooplankton and lowered phytoplankton biomass in Yellowstone Lake. Zooplankton supplied most of the N demanded by phytoplankton in Yellowstone Lake. Despite having similar biomass in the past, zooplankton excreted >200 times more NH_4^+ than cutthroat trout in Yellowstone Lake. Similarly, zooplankton were the main source of mineralized nutrients in the pelagic zone in other lakes (e.g., Scavia et al. 1988, Sarnelle and Knapp 2005). Lake trout indirectly decreased the excretion flux of zooplankton, because the assemblage shifted from being primarily composed of smaller copepods to being dominated by larger *Daphnia* species. Zooplankton have small body sizes and excreted at a higher mass-specific rate than trout (Hall et al. 2007).

Cutthroat trout affected nutrient cycling differently in Yellowstone Lake compared to Clear

Creek. In Clear Creek, our model results suggested that cutthroat trout affected nutrient cycling by increasing the flux of NH_4^+ available for uptake. Cutthroat trout consumed very few aquatic invertebrates in streams (L. Tronstad, *personal observation*) and did not affect algal biomass in this manner. However, constructing redds in spawning streams may decrease algal biomass, especially in the past when cutthroat trout were more abundant, as anadromous Pacific salmon did in Alaskan streams (Holtgrieve and Schindler 2011). Therefore, the direct effect of cutthroat trout was likely larger than their indirect effect in Clear Creek. Despite the different pathways in lakes and streams, fluxes were smaller in Yellowstone Lake than a tributary stream, because the density of cutthroat trout was much lower in Yellowstone Lake.

Invasive lake trout did not replace cutthroat trout as nutrient transporters in Yellowstone Lake and streams. Lake trout do not move nutrients between ecosystems, because they live and spawn within Yellowstone Lake. However, lake trout do transport nutrients within the lake by eating cutthroat trout in the epilimnion and excreting in the hypolimnion during summer stratification. Because predators are typically less abundant than their prey, we suggest that lake trout excrete far less N than cutthroat trout. Syslo et al. (2011) estimated that 340,000 lake trout lived in Yellowstone Lake in 2007. Given this estimate, lake trout with an average length of 500 mm TL (264 g M) would transport $7.0 \mu\text{g NH}_4^+ \text{N m}^{-2} \text{h}^{-1}$ to the hypolimnion, which is a small fish-derived flux.

Several characteristics of animals likely determine the degree to which they contribute to processes relative to nutrient demand. For example, animal fluxes can depend on the animal's density, biomass, and size distribution (Hall et al. 2007). Higher densities or biomass of fish generally means higher excretion fluxes in lakes (Griffiths 2006) and streams (McIntyre et al. 2008). High densities (43,000 fish/ha) of grey snapper (*Lutjanus griseus*) in the Bahamas excreted large amounts of N and P reducing nutrient limitation (Layman et al. 2011). Similarly, a low density of fish, such as cutthroat trout in Yellowstone Lake (51 fish/ha in 1998; Ruzycki et al. 2003), supplied little nutrients to primary producers. Larger individual body sizes also

tends to decrease mass-specific excretion fluxes (Hall et al. 2007). Cutthroat trout are relatively large fish which probably reduced the degree to which they contributed to N cycling relative to the same biomass of smaller-bodied fishes.

NH₄⁺ fluxes from cutthroat trout were large compared to other N fluxes in Clear Creek

The flux of transported nutrients from cutthroat trout in Clear Creek was similar or larger than fish-derived fluxes in other ecosystems. Excretion fluxes from cutthroat trout in Clear Creek were similar to NH_4^+ ($1400\text{--}4260 \mu\text{g N m}^{-2} \text{h}^{-1}$) and TDP ($90\text{--}387 \mu\text{g P m}^{-2} \text{h}^{-1}$) fluxes transported to coral heads by marine grunts (*Haemulon* spp.) resulting in increased coral growth (Meyer et al. 1983). Gizzard shad (*Dorosoma cepedianum*), a sediment feeding fish, transported ($1070\text{--}1690 \mu\text{g NH}_4^+ \text{N m}^{-2} \text{h}^{-1}$) a similar flux of NH_4^+ to the open water of Acton Lake, Ohio (Schaus et al. 1997) as cutthroat trout in Clear Creek. Cutthroat trout transported more NH_4^+ ($281\text{--}540 \mu\text{g N m}^{-2} \text{h}^{-1}$) and P ($35\text{--}95 \mu\text{g N m}^{-2} \text{h}^{-1}$) to Clear Creek when these fish were abundant compared to spawning Bonneville cutthroat trout and Kokanee salmon in Utah streams (Wheeler et al. 2014). Finally, cutthroat trout transported >13 times more nutrients to Clear Creek compared to waterfowl who transported terrestrial N ($205 \mu\text{g N m}^{-2} \text{h}^{-1}$) and P ($25 \mu\text{g P m}^{-2} \text{h}^{-1}$) to wintering wetlands in New Mexico (Post et al. 1998).

In contrast, nutrient transport by spawning Pacific salmon is often much higher than excretion fluxes from spawning cutthroat trout, because salmon die after spawning and their carcasses can fertilize streams (e.g., Bilby et al. 1996). Sockeye salmon (*Oncorhynchus nerka*) imported >50 times more N into Alaskan streams (Moore et al. 2007) compared to cutthroat trout excretion in Clear Creek. Similar to salmon, alewives (*Alosa pseudoharengus*; ~100–500 g wet mass/ind) die after spawning and their carcasses delivered $1880 \mu\text{g N m}^{-2} \text{h}^{-1}$ and $300 \mu\text{g P m}^{-2} \text{h}^{-1}$ to a pond in Rhode Island, USA (Durbin et al. 1979). Up to 67% of the P input by live alewives was from excretion fluxes (West et al. 2010). Unlike these fish, cutthroat trout may spawn several times during their life (Gresswell 1995). Spawning mortality varied between 13 and 31% in tributary streams of Yellowstone

Lake, but nutrients from decaying cutthroat trout carcasses probably had small effects on streams because river otters (*Lontra canadensis*) and grizzly bears (*Ursus arctos horribilis*) consume cutthroat trout (Crait and Ben-David 2006, Fortin et al. 2013), and we never observed carcasses decomposing in streams (L. Tronstad, *personal observation*). Similar to iteroparous suckers with low spawning mortality (Childress et al. 2014), excretion fluxes were likely the major nutrient source from spawning cutthroat trout.

The recent decrease in transported nutrients by spawning cutthroat trout may alter all trophic levels in Clear Creek through bottom-up effects. Cutthroat trout probably have minimal top-down effects on spawning streams, because these fish consumed few stream invertebrates (L. Tronstad, *personal observation*). However, excreted nutrients likely fertilized streams and were incorporated into the food web through uptake by stream microbes. Studies that experimentally fertilized streams had higher gross primary production, respiration, and algal biomass (Slavik et al. 2004, Benstead et al. 2009). Furthermore, isotopic evidence from studies of migrating fish showed that transported nutrients were incorporated into all trophic levels, including primary producers, invertebrates, and fish (Bilby et al. 1996, Childress et al. 2014). Finally, declining cutthroat trout in Yellowstone National Park negatively affected terrestrial and semi-aquatic predators such as osprey (*Pandion haliaetus*; Baril et al. 2013), river otters (Crait and Ben-David 2006), and grizzly bears (Fortin et al. 2013, Teisberg et al. 2014). The effects of fewer cutthroat trout may extend far from Yellowstone Lake because bears are eating more elk calves as spawning cutthroat trout become more scarce (Middleton et al. 2013).

Fish in streams can supply most of the N demanded by primary producers. In Clear Creek, cutthroat trout supplied up to 6.1% of the N demanded after these fish declined. Similarly, longfin dace (*Agosia chryogaster*) excreted 5–10% of the N demanded by stream microbes in Sycamore Creek, Arizona, USA (Grimm 1988a, Vanni 2002). Cutthroat trout likely supplied more N to stream microbes when they were abundant, similar to spawning Bonneville cutthroat trout and Kokanee salmon (46–188% of NH_4^+ demand; Wheeler et al. 2014). Fish excretion can dominate

fluxes, such as in Rio Las Marias, a Venezuelan stream that had extremely high fish biomass (McIntyre et al. 2008) and in Costa Rican streams where banded tetra (*Astyanax aeneus*) composed 18% of fish biomass but excreted 90% of P demanded by microbes (Small et al. 2011).

Based on model results, excretion fluxes from cutthroat trout supplied more NH_4^+ to stream microbes in the past when these fish were abundant compared to after cutthroat trout declined. Despite a presumed loss in uptake efficiency (lower v_f), more NH_4^+ was likely assimilated at higher NH_4^+ concentrations (higher cutthroat trout densities), because v_f decreased disproportionately slower than concentration increased (slope = -0.50). Similarly, more NO_3^- was assimilated at higher NO_3^- concentrations in streams across the USA, despite a loss in uptake efficiency as measured by declining v_f (Hall et al. 2009). Stream microbes likely retained more NH_4^+ in the past because cutthroat trout swam farther upstream at higher spawning densities. Spawning farther upstream allowed greater distance for an NH_4^+ molecule to be assimilated by stream microbes. However, our model did not predict total NH_4^+ uptake within Clear Creek, but only the amount of cutthroat trout-derived NH_4^+ removed. We did not observe nitrification in Clear Creek and we concluded that NH_4^+ was primarily taken up by microbes and not exported to the lake as NO_3^- . Overall, the model suggested that a larger amount of NH_4^+ from cutthroat trout was incorporated into spawning streams when cutthroat trout were abundant.

Conclusions

The abundance of Yellowstone cutthroat trout drastically declined following the invasion of lake trout, which strongly reduced nutrient mineralization in a tributary spawning stream. A compensatory response by other fish will not likely occur, because cutthroat trout are the only fish in these streams (however, the less abundant, nonnative longnose sucker spawns in a few tributaries of Yellowstone Lake) and other animals in the ecosystem cannot replace the role of cutthroat trout. Thus, after the introduction of lake trout in Yellowstone Lake, nutrient fluxes from cutthroat trout were greatly reduced in tributary streams. McIntyre et al. (2007) simulated how the random and nonrandom loss of

species can reduce nutrient cycling. Here we show a prediction from McIntyre et al. (2007), whereby the near extinction of a dominant species can reduce rates of nutrient cycling in an ecosystem. Reduced animal density or extinctions from invasive animal introductions can strongly reduce excretion fluxes from native animals.

Studies of the effects of dominant invasive animals have clearly shown that ecosystem processes can change in invaded ecosystems; however, we show that invasive animals can strongly alter an adjacent ecosystem. Scientists are only beginning to understand when and where invasive animals may contribute to ecosystem processes (Strayer 2012). Nutrient excretion by animals may contribute to a higher degree relative to demand when animal density is high, microbial demand is high, and nutrient concentrations are low (Vanni 2002, McIntyre et al. 2008). Our study generally agrees with this hypothesis; however, nutrient demand was moderate in the Yellowstone Lake ecosystem. Large changes in ecosystem processes can occur when invasive animals interfere with the movement of native animals. Flecker et al. (2010) discussed two ways in which migratory fish may alter ecosystems: material subsidies and process subsidies. Material subsidies are the transfer of nutrients, energy, or other resources that alter the resource pool in the recipient ecosystem. Conversely, process subsidies change process rates in the recipient ecosystem due to altered activities, such as feeding. Our results agree with Flecker et al. (2010) who hypothesized that material subsidies would strongly contribute to ecosystem processes when migrants have high biomass relative to the ecosystem size, the recipient ecosystem is relatively nutrient poor, and nutrients are readily taken up in the recipient ecosystem. In our study, the density of cutthroat trout and characteristics of the ecosystems by far had the greatest effect on when and where excretion fluxes from cutthroat trout contributed the most relative to demand. However, the degree to which animals contribute to nutrient cycling may vary in space, time, and by species (Vanni 2010). Invasive animals probably affect adjacent habitats in many ecosystems, especially if energy, material, or information are exchanged. We are only beginning to understand how the decline of cutthroat trout is cascading

throughout Yellowstone National Park (Middleton et al. 2013).

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