

Nonnative fish stocking alters stream ecosystem nutrient dynamics

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Abstract. Each year, millions of hatchery-raised fish are stocked into streams and rivers worldwide, yet the effects of hatchery-raised fish on stream nutrient cycles have seldom been examined. We quantified the influence of supplemental nonnative fish stocking, a widespread recreational fishery management practice, on in-stream nutrient storage and cycling. We predicted that supplemental, hatchery-raised brown trout (*Salmo trutta*) stocking would result in increased N and P supply relative to in-stream biotic demand for those nutrients and that stocked fishes would remineralize and store a significantly greater amount of N and P than the native fish community, due to higher areal biomass. To test these predictions, we measured the biomass, nutrient ($\text{NH}_4^+\text{-N}$ and soluble reactive phosphorus [SRP]) remineralization rates, and body carbon, nitrogen, and phosphorus content of the native fish community and trout stocked into four study streams. We then estimated fish growth rates to determine species-specific nutrient sequestration rates in body tissues for both stocked and native fish and measured ammonium and phosphorus uptake rates to determine the relative influence of net fish nutrient remineralization on stream nutrient cycles. When brown trout were stocked in these systems at density levels that were orders of magnitude higher than ambient native fish density, they provided a sizeable source of $\text{NH}_4^+\text{-N}$ that could account for up to 85% of demand for that nutrient. Stocked trout had minimal effects on in-stream SRP cycles even at high release densities, likely due to low per capita SRP excretion rates. A unique feature of our study was that we evaluated the temporal component of the stocked trout nutrient subsidy by estimating the number of fish removed from the system through natural mortality and angler harvest, which indicated that the stocked trout subsidy lasted approximately 6–8 weeks after stocking. By combining population models with areal nutrient excretion rates and estimates of biotic nutrient uptake, we showed that trout stocking provided a strong pulsed nutrient subsidy.

Key words: bottom up; conservation; fish stocking; fishery management; nitrogen; nonnative species; nutrient cycling; phosphorus; salmonids.

INTRODUCTION

A major threat to aquatic ecosystem conservation around the world is the introduction of nonnative fishes, both deliberate and unintentional. For instance, the introduction of relatively few species of exotic fish for recreational angling purposes has resulted in numerous extirpations of indigenous fish species worldwide (Cambray 2003). The impacts of introduced species are so widespread that approximately one-third of all endangered and threatened species in the United States are thought to have been harmed by introduced species (Bright 1999). Most studies examining large predator fish introductions have focused on top-down controls that regulate the abundance and composition of native species assemblages (Krueger and May 1991, Kerr and Grant 2000, Weidel et al. 2007), yet their influence upon ecosystem structure and function may pose a greater,

indirect threat because they “alter the fundamental rules of existence for all organisms in the area” (Vitousek 1986).

Many recent studies have shown that fish play important roles in ecosystem function (Taylor et al. 2007, Layman et al. 2011, Capps and Flecker 2013a, b, Griffiths and Hill 2014, Childress and McIntyre 2015). Fishes influence nutrient availability and primary production in freshwater ecosystems through nutrient sequestration in body tissues and nutrient remineralization via excretion and egestion (Vanni 2002). Fish biomass often constitutes a large ecosystem-scale pool of nutrients (Kraft 1992, Vanni et al. 2013) that can be a major driver of nutrient recycling in freshwater systems (Vanni and Findlay 1990, Schaus et al. 1997, Schindler and Eby 1997). Fishes are mobile, therefore the subsidy provided by their biomass can periodically enhance productivity in stream ecosystems through carcass decomposition, gametic deposition, and nutrient excretion (Gende et al. 2002, Naiman et al. 2002, Schindler and Parker 2002, Wilson and Xenopoulos 2011, Childress et al. 2014, Boros et al. 2015). Yet the strength of these interactions is determined by the amount and ratio of elements stored in body tissue and cycled through fish via remineralization (Elser 2006, Capps and Flecker 2013a). Consequently, ecological stoichiometry theory

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(see Sterner and Elser 2002) provides a useful framework for assessing impacts of introduced fishes on freshwater ecosystem function.

Recreational fishing is a major economic driver with an overall economic impact estimated to range from US\$69–US\$150 billion annually in the United States of America and Europe (Hickley et al. 1998). As a result, billions of dollars are spent each year to introduce large, often non-native, predator fish into streams and lakes through annual stocking of hatchery-reared fish that support recreational fisheries and enhance angling opportunities (Johnson et al. 1995). However, the potential impacts of stocking are now being reconsidered to take into account the maintenance of community diversity and ecosystem function (Eby et al. 2006). These considerations require a better understanding of how fishery management practices influence ecosystem processes and function.

The goal of this study was to examine the influence of nonnative brown trout (*Salmo trutta*) stocking on nutrient storage and cycling in streams in the north-eastern United States. Each year nearly 500,000 kg of trout and salmon are stocked into New York streams, often at densities much greater than sympatric native fish densities. We expected that these stocked fish would increase N and P supply relative to in-stream biotic demand for those nutrients. Furthermore, we predicted that stocked brown trout would remineralize and store a significantly greater amount of N and P than the native fish community, due to higher areal biomass. To test these predictions, we first estimated the biomass, nutrient (NH_4^+ -N and soluble reactive phosphorus [SRP]) remineralization rates, and body carbon (C), nitrogen (N), and phosphorus (P) content of the native fish community and stocked trout released into four study streams. We also estimated fish growth rates to determine interspecific nutrient source–sink dynamics for both stocked and native fish. Finally, we measured in-stream ammonium and phosphorus uptake rates to determine the relative influence of fish nutrient remineralization on stream nutrient cycles. Our findings reveal that supplemental fish stocking, a practice not previously considered in studies of nutrient cycling, can affect stream ecosystem function through alteration of in-stream nutrient cycles.

METHODS

Study streams

We quantified trout nutrient subsidies on four second–fourth-order streams (Big, East Koy, Kayaderosseras, and Meads Creeks) in upstate New York that receive annual stocked brown trout (*Salmo trutta*) in April and May each year. Nonnative brown trout are stocked at higher average biomass densities (220 g/m^2) when compared to resident, wild, brook trout (2.6 g/m^2), a closely related native salmonid fish found in these streams. The native fish community consists primarily of Catostomidae, Centrarchidae, Cyprinidae, Percidae, Cottidae, and Ictaluridae, along with naturalized populations of non-native brown and rainbow trout (*Oncorhynchus mykiss*) (hereafter referred to as “wild” trout). All trout released into the study streams were fin clipped by cohort from 2011 to 2013, enabling us to distinguish hatchery from wild trout and estimate growth rates. Angler surveys were also conducted on these streams from April to October 2011–2013 to estimate angler catch and harvest rates following methods outlined in Pollock et al. (1994). Ambient nutrient concentrations in the study reaches were moderate to low (Table 1), with mean stream discharge ranging from 344 to 976 L/s. Fish sampling took place from April to September 2012 through 2013, and dissolved nutrients were collected monthly during this period. Fish were captured and excretion rates were measured on a total of eight occasions in May–July in 2012 and 2013. Fish from each study stream were used in excretion rate trials. Uptake and turnover were measured on a single occasion for each stream in 2013 during the release period (i.e., within 1 month of stocking in April and May).

Biomass, apparent mortality, and angler harvest

We modeled fish population density and apparent mortality (i.e., mortality caused by natural processes, immigration, or angler harvest) of stocked trout using multiple pass depletions. Subsequent to stocking, electrofishing three-pass depletion population estimates (Bonar et al.

TABLE 1. Study stream characteristics.

Characteristic	Big	East Koy	Kayaderosseras	Meads
NH_4^+ -N ($\mu\text{g/L}$)	32 (1–105)	18 (15–22)	8 (0–19)	9 (8–10)
NO_3^- (mg/L)	1.8	2.7	0.12	0.3
SRP ($\mu\text{g/L}$)	10 (2–28)	5 (4–8)	3 (1–4)	6 (5–8)
Trout stocked	2860	12376	4320	3137
Depth (m)	0.19 (0.14–0.21)	0.50 (0.3–0.6)	0.27 (0.19–0.35)	0.23 (0.15–0.31)
Width (m)	7 (5–8)	10 (8–13)	12 (7–16)	8 (6–10)
Conductivity (μS)	635 (612–658)	333 (292–385)	224 (217–238)	204 (200–208)
Canopy cover (%)	49 (30–73)	48 (20–81)	51 (0–63)	8 (0–22)
In-stream cover (%)	29 (0–37)	20 (8–24)	13 (12–20)	13 (3–30)

Notes: Temperatures ranged from 12° to 21°C during our sampling period in 2012 and 2013. Ranges are provided in parentheses when the reported value is a mean. Note that NO_3^- (mg/L) was only sampled on one occasion after the study was concluded and is provided for reference only.

2009) were conducted in April and May then repeated in July and August on three study reaches in each stream. Sites selected for electrofishing were proximal to stocking locations and representative of the habitat within the study stream. Stocked trout densities were estimated by state agency personnel using standard procedures.

Stocked trout and native fish abundance was estimated via three-pass electrofishing (using a Leslie-DeLury binomial model; Leslie and Davis 1939, DeLury 1947) from fish captured using standard backpack electrofishing techniques (Bonar et al. 2009). Each stream section was isolated using blocking seines or natural features (shallow riffles) to survey a closed population compatible with depletion estimates. Population density (P_d) was calculated as $P_d = \hat{n}/a$ where, \hat{n} was estimated abundance and a was reach area (m^2). We weighed captured fish to the nearest gram and the estimated mean mass for each taxonomic family was multiplied by population density, yielding an estimate of areal biomass (g/m^2). Surveys were conducted during late spring and early summer 2012–2013.

Apparent mortality was estimated using a maximum likelihood estimation approach (negative log likelihood; Fournier et al. 2012). Model predictions were fit to observed values for fish cohort population density using a weighted residual sum of square structure for the density component taking the form of $RSS_{\text{density}} = \sum_{c,t} (\hat{D}_{c,t} - D_{c,t})^2$; where $\hat{D}_{c,t}$ is the predicted density of a cohort and $D_{c,t}$ is the observed density of that cohort at time t . The residual sum of squares for the harvest rate was similarly calculated, but was not divided by cohort, as anglers do not reliably observe whether fish are marked. This weighted residual sum of squares was then used to calculate the concentrated form of the negative log-likelihood $-\log \text{Likelihood} = (n/2) \ln(RSS/n)$; where n was the total number of observations in both fitted data sets.

Nutrient remineralization

We recorded fish mass (g) and fin clip type (to distinguish wild from stocked fish) for each captured fish. In order to account for handling stress, we identified the initial peak in excretion rates due to handling stress and fasting effects, and calculated where the exponential decay curve flattened out (half-life) following methods outlined in Whiles et al. (2009). Based on these findings,

fish were incubated in 1–5 L of stream water (depending on mass) for approximately 30 min to minimize handling stress response and to avoid oxygen stress and waste buildup (Whiles et al. 2009). A subset of fish from each captured taxon ($n = 1–35$ fish) were euthanized with MS-222 for analysis of C, N, and P percentage composition of body tissue.

Excretion rates were calculated based on the difference in dissolved ammonium (NH_4^+ -N) and SRP concentrations between identical containers with and without fish. Ammonium was quantified using fluorometric methods (Taylor et al. 2007). We determined SRP concentrations based on the reaction of the orthophosphate ion (PO_4^{3-}) with ammonium molybdate and antimony potassium tartrate in an acid medium (Stainton et al. 1977). Excretion rates were expressed in terms of micromole nutrient (NH_4 or SRP) per gram of fish per hour. We calculated volumetric excretion (E_v , mole nutrient per unit volume) as $E_v = (E_a \times A \times T)/V$, where E_a is areal excretion rate ($mol \text{ nutrient} \cdot m^{-2} \cdot h^{-1}$), A is reach area ($length \times width, m^2$), T is travel time (minutes) through each reach, and V is volume ($length \times cross\text{-}sectional \text{ area}, m^3$) at a given discharge (McIntyre et al. 2008, Benstead et al. 2010).

Expected densities were projected by multiplying the initial population of each taxa by the estimated apparent mortality rate. Expected densities were then combined with field measurements of nutrient excretion to calculate whole-reach estimates of areal nutrient excretion by trout in each stream over time. Areal fish-mediated nutrient recycling was calculated as the product of estimated population biomass (g/m^2) and excretion rates ($\mu mol \cdot g^{-1} \cdot h^{-1}$).

Growth rates for stocked trout were calculated as the mean change in weight over time for a given cohort. For the native fish assemblage, growth was calculated as the mean change in areal biomass over time. We calculated storage rates of C, N, and P as the change in the product of areal biomass estimates (i.e., change in mean mass [g] from time t to $t + 1$) and percentage element in fish tissues. Percentage body elemental (C, N, and P) content was analyzed using a CONFLO-III Elemental Analyzer, Thermo Electron Corporation, Bremen, Germany by the Cornell University Nutrient Analysis Laboratory on a subset of fish (Table 2) caught in May and July 2013. We then subtracted the amount of nutrients produced via areal excretion from the amount of nutrients stored in fish tissues to determine whether taxa were operating as net sinks or net remineralizers (i.e., subsidies) of nutrients (Capps and Flecker 2013a).

TABLE 2. Mean areal NH_4^+ -N and SRP stocked trout and native fish assemblage excretion rates for each study stream during the stocking period (April–May) in 2012 and 2013.

Stream	Stocked ($\mu mol \cdot m^{-2} \cdot h^{-1}$)		Native ($\mu mol \cdot m^{-2} \cdot h^{-1}$)	
	NH_4^+ -N excretion	SRP excretion	NH_4^+ -N excretion	SRP excretion
Big	135.38	0.40	0.81	0.18
East Koy	129.01	0.29	1.67	0.06
Kayaderoseras	78.65	0.21	0.68	0.23
Meads	123.75	0.12	0.63	0.13

Water chemistry and N uptake

Stream water was analyzed for SRP and $\text{NH}_4^+\text{-N}$ using standard methods (Taylor et al. 2007). Uptake of N and P was measured using short term addition of $\text{NH}_4\text{Cl-N}$ and $\text{KH}_2\text{PO}_4\text{-P}$ solutions, along with NaCl as a conservative tracer once per stream in summer 2013 (Tank et al. 2008). Water samples were then collected downstream of the injection point when elevated concentrations reached a plateau. We calculated solute (S) uptake length (S_w) using an exponential decay model, $S_w = \ln S_0 - kx$, where S_0 was the background corrected plateau solute concentration at x m downstream from the injection point, and k was the exponential decay rate (Stream Solute Workshop 1990). The decay rate was calculated by plotting the natural log of the S tracer/conservative tracer and the distance from the injection site (m) and S_w is calculated as the inverse of the decay rate. Uptake length is influenced by discharge (Webster and Valett 2006), so we calculated S uptake velocity ($\text{m}^{-1}\cdot\text{min}^{-1}$) using the equation: $V_f = Qk/w$; where Q is discharge ($\text{m}^{-3}\cdot\text{min}^{-1}$) and w is mean stream wetted width. Finally, we calculated an areal S uptake rate (U) using the equation $U = V_f S_b$, where S_b is the background S concentration prior to release. We calculated excretion turnover distance (m; i.e., the distance required for excretion to turn over the ambient nutrient pool completely) by dividing ambient nutrient concentration by E_V and multiplying by the reach length (m) for which E_V was calculated (Benstead et al. 2010).

Statistical analysis

To test for differences between native fish influence on stream nutrient cycles and the influence of stocked trout, we used a mixed-effect model analysis of variance (ANOVA) where areal excretion rates was the dependent variable, fish origin (hatchery or native) was the treatment variable (fixed), and family, time (sampling date), temperature, and stream were random factors (Pinheiro and Bates 2000). We analyzed the effect of fish family on mass specific excretion rates and molar N:P excretion using a generalized linear model (GLM). We also assessed the relationship between time of year and temperature with excretion rates using GLM. Significant differences among factors were followed by Tukey Honestly Significant Difference (HSD) tests. We used QQ plots and a Shapiro-Wilk test to visually and analytically examine, respectively, whether our sample came from a normally distributed population. Where data were not bivariate normal, we used appropriate log transformations. We tested for homogeneity of variance using a Levene's test. Results were considered significant when $P < 0.05$. All statistical analyses were conducted in Program R version 2.15.2 (R Core Team 2013).

RESULTS

Log-transformed per capita body-mass-specific $\text{NH}_4^+\text{-N}$ and SRP excretion rates were lower for stocked trout than for most native fish species with the exception of Cottidae for both nutrients and Ictaluridae for $\text{NH}_4^+\text{-N}$ only (Fig. 1). We did not find a significant difference in areal SRP

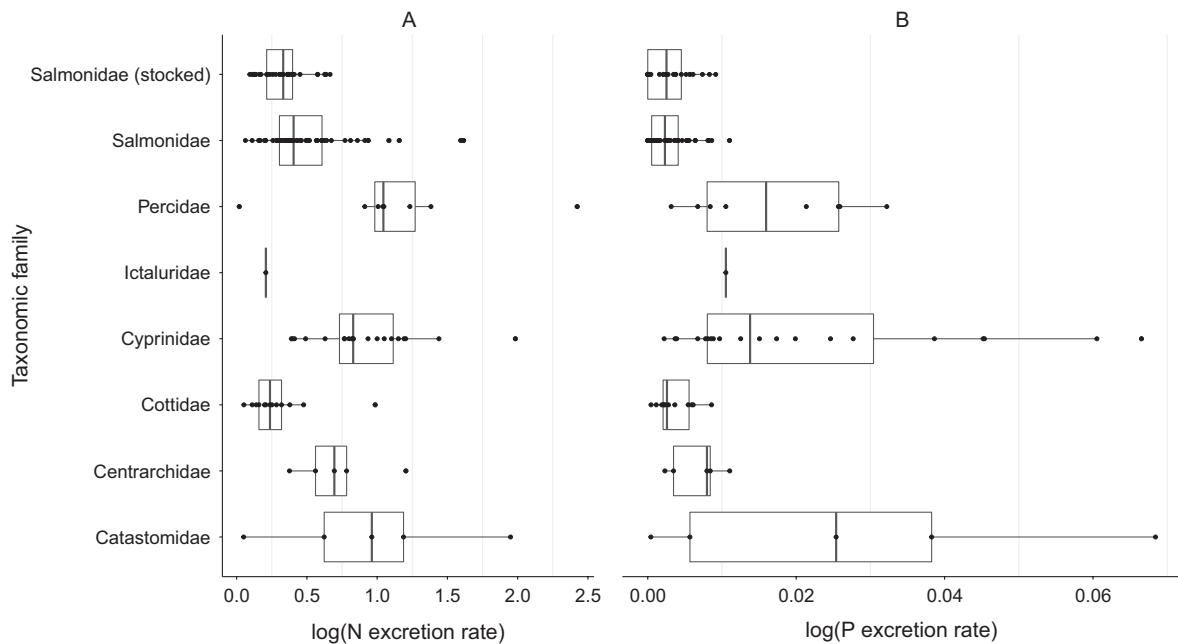


FIG. 1. Boxplot of the (A) N and (B) P mass-specific excretion rates (measured as $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) for each taxonomic family found in the study streams. The middle line of the box shows the mean, the outer edges show the 25th and 75th percentiles, and the whiskers represent 1.5 times the interquartile range.

excretion between stocked ($0.25 \mu\text{mol SRP}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) and native fish ($0.15 \mu\text{mol SRP}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$; $P = 0.11$; $F = 2.35$; Table 2). There was a significant positive relationship between $\text{NH}_4^+\text{-N}$ excretion and time of year ($P < 0.001$; $t = 17.71$) and temperature ($P < 0.001$; $t = 44.67$). Though there was a significant relationship between excretion and temperature, the effect size is small compared to total biomass. Moreover, all fish experienced the same temperatures, thus differences in relative excretion rates would not be affected. The pattern was the same for SRP and time of year ($P = 0.04$; $t = 4.25$) but there was not a significant relationship between SRP excretion and time of year ($P = 0.6$; $t = 0.30$). Log molar N:P excretion was greater for fish of hatchery origin (1.80 log N:P molar) and wild fish (0.76 log N:P molar; $P = 0.03$; $t = 2.20$).

Hatchery brown trout were stocked at an areal biomass (220 g/m^2) that was approximately one order of magnitude greater than the native fish assemblage (2.6 g/m^2). However, the initially high areal biomass of hatchery trout decreased considerably after stocking in April and May to levels at or below that of the native fish

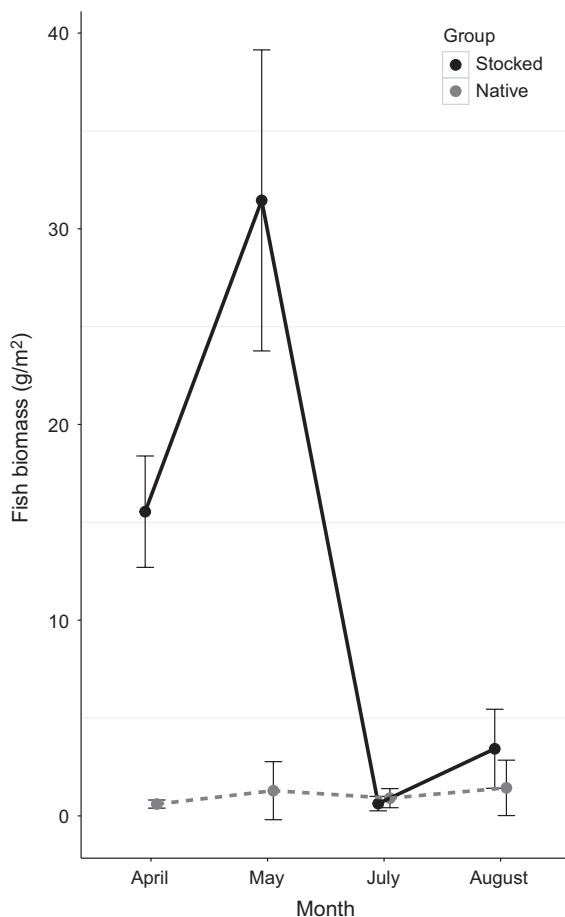


FIG. 2. Estimated native and stocked fish biomass during study months averaged for 2012 and 2013 and across the four study streams. Note that stocking took place in April and May in both years.

assemblage (Fig. 2) due to high apparent mortality (mean annual mortality rate = 0.99) and angler harvest (mean harvest rate (April–October) = 6.80 fish/ha) rates. Due to their greater areal biomass, mean stocked trout $\text{NH}_4^+\text{-N}$ areal excretion rates ($117 \mu\text{mol NH}_4^+\text{-N}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) at release densities were significantly greater ($P < 0.001$; $F = 9.30$) than the entire native fish assemblage combined ($0.94 \mu\text{mol NH}_4^+\text{-N}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$; Table 2).

Nutrient uptake rates averaged $220 \mu\text{mol NH}_4^+\text{-N}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ and $13 \mu\text{mol SRP}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$ across the four study streams. Areal excretion by stocked trout at release was thus equivalent to an average of approximately 55% (range 39–85%) of the $\text{NH}_4^+\text{-N}$ demand in the four study streams while native fish areal excretion only comprised an average of approximately 0.5% of $\text{NH}_4^+\text{-N}$ demand (Fig. 3), despite slightly lower per capita nutrient excretion rates for stocked trout. The difference in the proportion of $\text{NH}_4^+\text{-N}$ demand accounted for by stocked trout was significantly higher than the native species assemblage combined ($P < 0.0001$; $F = 4373.94$). Conversely, neither stocked trout nor native fish accounted for a major proportion of SRP demand in the study streams, however, the difference was significant between the two groups ($P = 0.0003$; $F = 13.00$). Stocked trout SRP excretion only comprised an average of 0.3% of SRP demand, which was comparable to the 0.22% of SRP demand accounted for by excretion from the native fish assemblage (Fig. 3). The presence of stocked trout significantly reduced the excretion turnover distance of $\text{NH}_4^+\text{-N}$ relative to that of the native fish community ($P < 0.001$; $F = 344.90$; Fig. 3). Conversely, the distance required for both native and stocked trout excretion to completely turn over the ambient SRP pool was large (mean fish assemblage SRP turnover = 9.86 km; Fig. 3), indicating that fish influence on SRP cycles was negligible. The influence of stocked trout nutrient excretion on stream nutrient cycles declined over time as biomass decreased (Fig. 4) due to high mortality rates combined with angler harvest.

Both stocked and wild trout showed no appreciable growth (Table 3). Some native fishes had discernible growth rates, while others showed no appreciable growth (Table 3). We determined net nutrient remineralization by subtracting the nutrients remineralized via excretion from the nutrients sequestered in fish tissues, organs, and scales through growth. At release densities, net stocked trout nutrient remineralization was a major $\text{NH}_4^+\text{-N}$ source (Fig. 5), though this subsidy diminished by mid-summer due to the decrease in biomass over time (Fig. 4) and was not a major source of SRP (Fig. 4). Although salmonids did not appear to be a net sink of either N and P, we found that suckers (Catastomidae) and to a lesser extent sculpins (Cottidae) provided substantial sinks of N and P relative to other fish taxa.

DISCUSSION

Our results suggest that fisheries management practices such as fish stocking influence community-wide recycling and nutrient availability. The native fish assemblage had

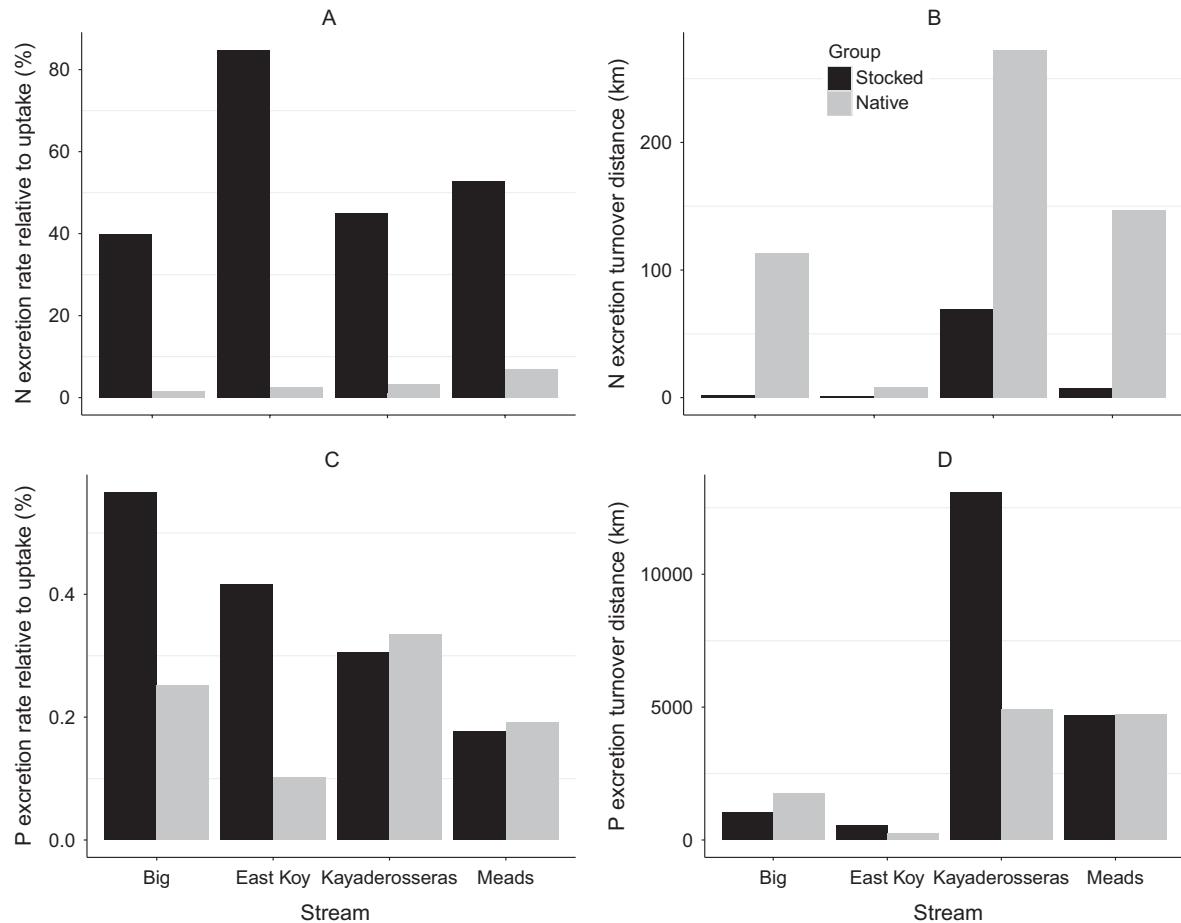


FIG. 3. (A and B) Areal N and P excretion relative to uptake (%) and (C and D) N and P excretion turnover distance for native and stocked fish at release densities. All samples for these analyses were taken within 1 month of stocking.

limited effects on $\text{NH}_4^+\text{-N}$ or SRP nutrient cycles at natural densities. However, when nonnative fish were added to these systems at biomass levels that were orders of magnitude greater than ambient native fish biomass, these stocked fish provided a sizeable source of $\text{NH}_4^+\text{-N}$ that could account for up to ~85% of in-stream biotic demand for that nutrient. Stocked trout had minimal effects on in-stream SRP cycles even at high release densities, likely due to low per capita SRP excretion rates.

Fish often represent the dominant pool of particulate nutrients when abundant (Capps and Flecker 2013a, Vanni et al. 2013). Trout are often stocked at much higher biomass levels than resident fish and therefore can alter the location, concentration, and storage duration of in-stream nutrients. We confirmed that under conditions of low to moderate ambient nutrient concentrations, such as the streams in this study, fish nutrient recycling through remineralization provided an important nutrient flux (Vanni 2002, McIntyre et al. 2008, Warren and McClure 2012). At release densities, stocked trout provided a substantial $\text{NH}_4^+\text{-N}$ process subsidy (up to ~85%) that was orders of magnitude greater than the native fish

community subsidy. The $\text{NH}_4^+\text{-N}$ process subsidy provided by stocking of hatchery fish (39–85% of demand) falls mostly within the range provided by migratory native fish populations (46–188%; Wheeler et al. 2015). This finding indicates that fisheries management practices that introduce nonnative predators into streams have the potential to influence basal resource availability and ecosystem function, beyond the direct effects to the system through predation and competition that have been previously documented (Flecker and Townsend 1994, Cambray 2003, Baxter et al. 2004).

SRP subsidies mediated by stocked trout accounted for a relatively low proportion (<1%) of biotic demand, despite high biomass levels. This difference was likely due to the relatively low amount of SRP excreted by salmonids in this study. Of all taxa surveyed, salmonids had among the lowest per capita SRP excretion rates along with Cottidae, suggesting a dietary P limitation, as nutrient availability must meet the assimilatory demands of the consumer (McManamay et al. 2010). SRP excretion rates were much lower for all taxa when compared to $\text{NH}_4^+\text{-N}$ excretion, constituting a minimal fish-mediated

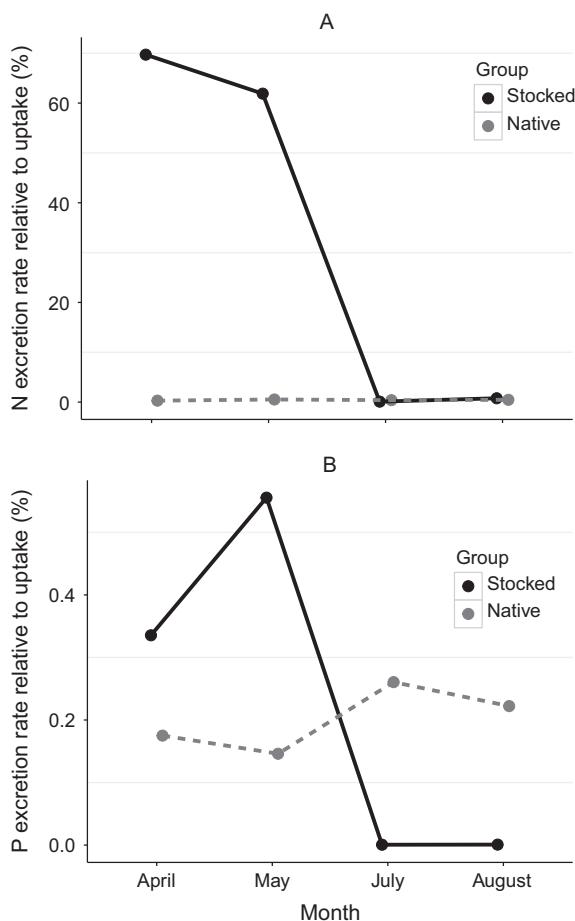


FIG. 4. Percentage of in-stream (A) $\text{NH}_4^+\text{-N}$ and (B) SRP demand accounted for by stocked trout and native fish over time. Trout were stocked in April and May.

nutrient flux as expected given the higher molar weight of P. Still, log molar N:P ratios from fish in this study (mean log N:P molar = 0.96) was comparable to that of other studies of fish assemblage excretion in eastern North American freshwater streams (McManamay et al. 2010). This dichotomy between $\text{NH}_4^+\text{-N}$ and SRP excretion has been previously observed. For example, Moslemi et al. (2012) found that N excretion by an aquatic snail species (*Tarebia granifera*) could account for up to 16% of biotic N demand, but P inputs from excretion did not account for discernible percentage of biotic P demand. Griffiths and Hill (2014) found similar results where another aquatic snail species (*Elimia clavaeformis*) accounted for an average of 58% of stream water ammonium concentrations yet supplied only 1% of SRP concentrations.

We incorporated the temporal component of stocked trout nutrient subsidies by estimating the number of fish removed from the study streams through apparent mortality and angler harvest. By combining population dynamics models with areal nutrient excretion rates and estimates of biotic nutrient uptake, we showed that trout stocking provided a pulsed nutrient process-subsidy that

TABLE 3. Fish percentage C, N, and P content and estimated mean daily growth rate for the most common taxonomic families found in the four study streams.

Family	% C	% N	% P	Mean growth ($\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)
Catostomidae (38,5)	41.8	9.6	3.5†	0.0223
Centrarchidae (33,4)	40.5	10.9	4.2	0.0003
Cottidae (51,13)	40.2	8.4	4.0	0.0016
Cyprinidae (203,26)	42.9	10.0	3.0	0.0001
Ictaluridae (13,1)	41.8	9.9	3.1	0.0054
Percidae (32,5)	40.6	9.6	3.3	0.0000
Salmonidae (stocked; 303, 22)	46.3	10.6	1.8	0.0000
Salmonidae (60, 13)	45.1	11.5	2.1	0.0000

Notes: Sample size for growth rate estimation followed by sample size of the randomly selected subset of captured fish used for body elemental content analysis is given in parentheses.

† Percent body phosphorus value for Catostomidae from McIntyre and Flecker (2010).

diminished over time due to high apparent mortality rates. The nutrient subsidy provided by stocking lasted for approximately 6–8 weeks, similar to the amount of time migratory fish (e.g., salmon) provide important nutrient subsidies to recipient streams (Naiman et al. 2002). These pulsed subsidies can have important implications for stream function, as ecosystems are often sustained either by continuous nutrient subsidies or large magnitude nutrient pulses (Weber and Brown 2013). Fish-mediated nutrient pulses have also been linked to decreased water clarity, increased productivity, changes in zooplankton and macroinvertebrate densities, and spatial alteration of macrophyte coverage (Weber and Brown 2013, Childress and McIntyre 2015).

Nutrient concentrations in streams can vary considerably across short distances (e.g., Dent and Grimm 1999). In addition to providing a nutrient subsidy through remineralization, the practice of trout stocking can alter the spatial dynamics of nutrient cycles by creating biogeochemical hotspots (McIntyre et al. 2008). Following release into streams, stocked trout temporarily form large aggregations that are eventually reduced through emigration, angler harvest, and natural mortality (Alexiades et al. 2014). These aggregations can create areas of enhanced biogeochemical activity (Capps and Flecker 2013a, b) and may temporarily displace native fish (Alexiades et al. 2014), further altering nutrient dynamics. In this study stocked trout significantly altered the distance required to turn over the ambient SRP and $\text{NH}_4^+\text{-N}$ pools relative to the native fish community, further impacting the spatial dynamics of nutrient cycles.

We accounted for elemental storage in body tissues and growth rates in addition to nutrient remineralization to provide a more realistic estimate of the net ecosystem effects of nutrient subsidies from stocked trout and elucidate the influence of native fishes on nutrient source-sink dynamics in freshwater streams. In these study streams, growth rates and elemental composition varied

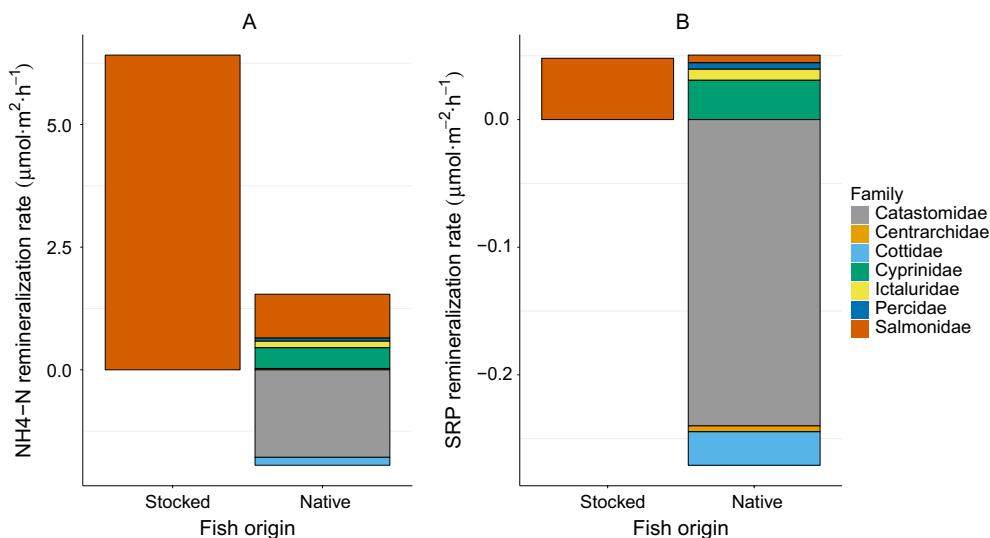


FIG. 5. Net (A) N and (B) P remineralization rates by stocked hatchery trout and the native fish assemblage delineated by taxonomic family and averaged across the study streams and years. Positive values indicate that taxa are acting as net nutrient recyclers via remineralization while negative values indicate that taxa are net nutrient sinks via sequestration in body tissue. [Color figure can be viewed at wileyonlinelibrary.com]

considerably among taxa. When we combined nutrient recycling with estimates of sequestration in body tissues we saw that some taxa provided a net nutrient source (*Cyprinidae*, *Ictaluridae*, *Percidae*, *Salmonidae*) while others were nutrient sinks (*Catastomidae*, *Centrarchidae*, *Cottidae*). Recent research examining the role of animals as nutrient sources or sinks shows that a large nutrient pool size does not necessarily equate to a nutrient sink; instead, population dynamics determine whether animals are sources or sinks (particularly changes in population biomass; Vanni et al. 2013). We addressed this by measuring species-specific growth and mortality to determine whether fishes in our study streams are operating as a net source or sink of nutrients.

Although we found that trout stocking can provide a substantial nutrient subsidy, a potential limitation to our estimation of net nutrient remineralization was that we did not estimate carcass decomposition or gametic deposition (Childress and McIntyre 2015). While the native fish community likely provides additional nutrient subsidies through these processes, carcass decomposition and gametic deposition are likely not relevant for stocked trout. Few stocked trout survive long enough to spawn and there is minimal instream carcass decomposition due to angler harvest and high avian predation rates (Stiller 2011). Thus, our approach is likely capturing the most important processes involved in stocked trout mediated stream nutrient dynamics. Another potential limitation of this study was that uptake dynamics were only measured once, thus providing only a snapshot the ecosystem nutrient budget, which could vary substantially over time. Future studies should consider long-term monitoring of uptake dynamics in freshwater streams.

Management and conservation implications

Fish can be a major driver of N and P nutrient recycling in freshwater systems (Schaus et al. 1997, Schindler and Eby 1997, Vanni 2002). Nevertheless, stream fishery managers and ecologists often overlook the potential influence of fish on in-stream nutrient cycles. While this study was only the initial step in understanding the potential mechanisms by which stocking nonnative fish can affect stream nutrient cycles, managers could implement approaches to minimize the potential for impact. For example, harvest rates, not just catch rates, should be considered when determining the number of fish to stock. In our study streams, angler harvest and avian predation appear to remove the majority of these fish, thereby minimizing the potential for nutrient addition through carcass decomposition and long term excretion subsidies. However, in stream sections where catch and release regulations apply, no removal of fish would occur from angling, therefore we would expect process and material nutrient subsidies to increase.

Although the streams in this study were mid-order (second–fourth order) with at least some agricultural or urban land use within the watershed, the process subsidy provided by stocking could account for a relatively large proportion of N demand. This effect would be compounded in higher order headwater streams that might be more nutrient-poor than our study streams. Therefore managers might consider limiting stocking in high-order nutrient-limited streams (or mountain lakes; see Eby et al. 2006). Though recreational angling provides economic and societal benefits, recreational fisheries that are supported through supplemental fish stocking should also be considered in terms of their impacts upon native species and ecosystem function.

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DATA AVAILABILITY

Data associated with this paper are available in figshare: <https://doi.org/10.6084/m9.figshare.4488389.v1>