Multiple nutrient subsidy pathways from a spawning migration of iteroparous fish

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SUMMARY

1. Migratory animals can enhance ecosystem productivity through the delivery of material subsidies. Among fish, Pacific salmon are well known to deliver large quantities of nutrients to streams as they die after spawning, but the input pathways by which iteroparous species provide nutrient subsidies have not been resolved.

2. Our objective was to determine the importance of excretion, eggs and carcasses as nutrient sources from a large migration of longnose suckers into a stream draining a moderately agricultural catchment. Additionally, we evaluated nutrient limitation in the stream using nutrient-diffusing substrates and determined the timing of nutrient releases during egg decomposition using a microcosm experiment.

3. Eggs were the largest component of the nitrogen (N, 57%) and phosphorus (P, 76%) inputs from the migration, followed by excretion by live adults (40% N, 16% P). Carcasses were a minor component of inputs.

4. Estimated P inputs from fish were over three times larger than the observed export of dissolved P in this P-limited stream during the 66-day sampling period. In contrast, sucker N inputs were <2% of dissolved N export, which was dominated by NO_3. However, the dynamics of NH_4 concentrations through the course of the migration were closely associated with estimated NH_4 inputs from excretion and eggs.

5. Eggs and excretion constitute significant nutrient inputs during migrations, even in catchments with elevated nutrient loads from agriculture. Mass mortality is not required for migratory fish to enhance nutrient availability in their spawning habitats.

6. Given that sucker excretion rates and female reproductive investment are typical for freshwater fish, our results suggest that spawning migrations of iteroparous species in rivers around the world may deliver important nutrient subsidies when migrations are large.

Keywords: fish excretion, migratory fish, nitrogen, nutrient subsidy, phosphorus

Introduction

Material transfer across ecosystem boundaries can enhance productivity in recipient ecosystems (Polis, Power & Huxel, 2004). The ecological importance of subsidies depends on their size and form as well as the background availability of resources in the recipient system (Marczak, Thompson & Richardson, 2007). Animals can be important nutrient and energy vectors as they move among habitats to feed or reproduce, delivering materials through waste products, gamete deposition or mortality. Each of these sources can be major inputs to recipient ecosystems. For example, reef fish transfer nutrients from feeding to refuge habitats as they excrete during diel movements (Meyer, Schultz & Helfman, 1983), sea turtles deposit energy- and nutrient-rich eggs on beaches (Bouchard & Bjorndal, 2000) and emergent aquatic insects provide prey subsidies to riparian predators (Nakano & Murakami, 2001). Many fish species migrate in large numbers to spawn in habitats that are distinct from those where growth and gamete production occur. As Pacific salmon migrate from the ocean to

fresh waters to spawn, they deliver large quantities of nutrients and energy to their spawning grounds (Janetski *et al.*, 2009).

Understanding how life history may alter the role of migratory fish in delivering nutrient subsidies is important for determining the generality of this phenomenon. Most Pacific salmon are semelparous, dying after spawning once, whereas most migratory fish worldwide are iteroparous (Flecker *et al.*, 2010), spawning multiple times. Because iteroparity sharply reduces the input of adult carcasses, this aspect of life history variation may affect the quantity and type of materials delivered during spawning migrations. Migrations of iteroparous suckers (Catostomidae) create large nutrient pulses resulting in increased algal and invertebrate growth (Childress, Allan & McIntyre, 2014), suggesting that fish migrations can provide subsidies through excretion and gametes without large carcass inputs.

Egg deposition during spawning fish migrations may be a broadly important nutrient pathway because fish eggs are energy- and nutrient-rich and have low survival rates (Dahlberg, 1979). As such, fish eggs are an important food source for many fish and invertebrates (Orians & Janzen, 1974; Dahlberg, 1979). For instance, resident trout and juvenile salmon sometimes eat large quantities of salmon eggs (Moore, Schindler & Ruff, 2008; Denton *et al.*, 2010), which can drive most of their annual growth (Bentley *et al.*, 2012). Because female fish can invest as much as 30–70% of body mass in eggs (Moyle & Cech, 2004) and spawn many times during their lifetime, the deposition of gametes can regenerate large quantities of nutrients.

Fish excretion can also contribute substantially to nutrient supply in aquatic ecosystems (Vanni, 2002). Even during salmon migrations, which have large carcass inputs, the dynamics of dissolved nutrient availability are more closely associated with the number of live salmon than carcasses (Tiegs *et al.*, 2011). Similarly, excretion from anadromous alewife provides nutrients to Atlantic coastal ecosystems (Durbin, Nixon & Oviatt, 1979; Post & Walters, 2009). Fish that become highly concentrated during migration are likely to deliver substantial quantities of nutrients via excretion (Flecker *et al.*, 2010).

Community responses to resource subsidies depend on the background availability of comparable resources in the ecosystem (Marczak *et al.*, 2007). Agricultural activities tend to increase in-stream nutrient concentrations (Vitousek *et al.*, 1997; Baker & Richards, 2003); thus, the catchment context will alter the relative magnitude of background and subsidy nutrients. However,

resident fish can still recycle significant quantities of nutrients in streams draining highly agricultural catchments when fish biomass is high (Wilson & Xenopoulos, 2011). The importance of nutrients from migratory fish in such contexts is largely unknown and will depend on whether nutrients limit productivity and on the relative magnitude of anthropogenic and fish-derived nutrients.

In this study, we sought to determine whether iteroparous species can deliver ecologically important quantities of nutrients in a stream draining an agricultural catchment, in spite of low mortality. We examined this by quantifying the inputs from the three pathways – carcasses, eggs and excretion – during a large migration of longnose suckers (*Catostomus catostomus*). Suckers migrate to spawn in streams across North America, often reaching very high densities. Migrations of longnose and white suckers (*Catostomus commersonii*) into Great Lakes tributaries range from 10^2 to 10^4 individuals in small streams to 10^5–10^6 in large rivers (Klingler, Adams & Heinrich, 2003; Burtner *et al.*, 2011; Childress *et al.*, 2014). These large migrations can deliver nutrients that dominate nutrient fluxes in oligotrophic streams and increase algal and insect growth (Childress *et al.*, 2014). To evaluate the ecological relevance of these inputs in an agricultural setting, we compared the size of sucker nutrient inputs to stream nutrient export during the migration.

Methods

We estimated the timing and magnitude of nutrient inputs from a large spawning migration of longnose suckers in Lily Bay Creek (44.8470 N, 87.2673 W), Door County, Wisconsin during March–June 2013. Lily Bay Creek is a second-order tributary to Lake Michigan. The catchment is 70% agricultural, mostly in pasture or hay but with 20% row crop coverage and at least one dairy operation. The riparian zone is largely forested, particularly in the downstream reaches, which have substantial stocks of large woody debris. The stream is low gradient and sinuous with sand and silt substrates between cobble-bottomed riffles. Discharge during the study period averaged 0.29 m^3 s^{-1}. Water level and temperature were logged every 6 min using a HOBO® U20 (onsetcomp. com); we converted water level to discharge using a power–function relationship between water level and discharge based on discharge measurements across a range of water levels ($n = 12$, $r^2 = 0.97$).

To determine background nutrient levels and nutrient dynamics associated with the sucker migration, we sampled stream water daily for 66 days. Samples were

collected 200 m upstream of the stream mouth to reflect catchment nutrient export. Samples were filtered in the field (Whatman GF/F; 0.7 μm pore size), promptly placed on ice and analysed for ammonium (NH_4) by fluorometry (Taylor *et al.*, 2007) within 48 h or frozen for later analysis of nitrate (NO_3) and soluble reactive phosphorus (SRP) by standard colorimetric methods (APHA, 1998).

We determined fish movement and the number of fish in the stream by separately capturing fish migrating upstream and downstream in two back-to-back trap nets that spanned the full width of the stream. Suckers began migrating in 2013 at temperatures (*c.* 2 °C) well below those previously observed (*c.* 7 °C), and we estimate that the migration began 2 days before we installed the nets. Nets were emptied daily for 6 weeks until no fish were captured on three consecutive days. To enable recapture identification, we marked the dorsal fin of all upstream migrants using a hole-punch across a fin ray. Fish that entered the stream prior to the installation of trap nets (i.e. outgoing fish that were unmarked) were assumed to have entered in equal numbers on the 2 days before installation because suckers were observed in a nearby stream with a similar temperature regime on those days. We removed fish from nets daily and released them after determining sex and species for all fish captured and measuring total length (TL) for fish within logistical limits with an average sample size of 187 when catch exceeded measurement capacity. We also measured wet mass for a subset of fish whose length was measured (*n* = 190).

We measured excretion rates for 38 longnose suckers by incubating live fish in plastic basins containing 20 L of fresh, unfiltered stream water for 15 min, then comparing pre- and post-incubation concentrations of dissolved N and P. Incubations were carried out on 4 days to capture a range of stream temperatures (4.9–12.5 °C). We chose a short incubation time for these large fish to avoid oxygen stress; suckers reduced oxygen concentrations quickly during incubations (up to 8 mg L^{-1} h^{-1}; E. S. Childress, unpubl. data), which would impose substantial stress over the longer incubations that are otherwise preferable (Whiles *et al.*, 2009). We fit a predictive model of measured per capita excretion rates (log-transformed) as a function of total length (log-transformed) and water temperature. Three males were high outliers in P excretion, and were excluded from the statistical analysis. We estimated total daily N and P excretion by the sucker population by estimating individual excretion in 6 min time steps from temperature records and size-frequency distributions of body total length and summing across all individuals.

We estimated nutrient inputs from eggs by applying body length–ovary mass relationships to the length frequency distribution of females and multiplying by the nutrient content of eggs and their mortality rate. Based on dissections of emigrating females, we assumed that all eggs were spawned. We measured ovary mass of 51 females as they entered the stream, and fit log_e of ovary wet mass to log_e of female body length using linear regression. We assigned a length to females that were not measured by randomly sampling the overall size distribution with replacement. The water content of eggs was determined by mass loss during oven-drying (60 °C, 48 h). Homogenised subsamples from nine ovaries were analysed for N content using an elemental analyser (Gas-Bench II; Thermo Scientific™, Waltham, MA, USA) and for P content by colorimetric analysis of SRP following hydrochloric acid digestion. Egg survival to larval emigration, based on daily drift sampling during larval out-migration, was 11% (E. S. Childress, unpubl. data). Mean estimates with 95% confidence intervals were developed for ovary wet mass, ovary N and ovary P using bootstrapping (10 000 replicates) by resampling the distributions of TL for fish with unknown length, including prediction error from the TL-ovary mass regression and resampling from distributions of observed moisture content and nutrient content (see Appendix S1).

To estimate the timing of nutrient regeneration during egg decomposition, we conducted a microcosm experiment. Freshly stripped eggs (0.20 g wet mass) were placed in 1-L jars (*n* = 45) with 0.9 L of stream water and mesh tops that excluded debris but allowed for gas exchange. Three jars were incubated without eggs as controls. Jars were placed in flow-through containers along the stream bank such that they were continuously bathed in stream water to simulate the stream temperature but were sealed from exchange with the water. Jars were destructively sampled daily for water chemistry (SRP, NH_4 and NO_3 as above). Three jars were sampled for the first 10 days, and two were sampled thereafter to extend the duration of the experiment. Control jars were sampled at the beginning and end of the experiment. Algae bloomed in the egg jars by the end of the experiment, so uptake likely reduced the detection of nutrient regeneration. However, the experiment provides an estimate of the timing of nutrient release. The timing of nutrient regeneration from eggs in the stream was estimated from the mean daily nutrient increase per mass of eggs (decreases were excluded) in the experiment combined with estimates of daily egg deposition. Based on the observation that females left in large numbers on the first day after we observed spawning, each female's

eggs were assumed to have been deposited the day before emigration.

To allow for comparison of sucker inputs and stream concentrations, daily excretion and egg inputs were divided by discharge rate yielding a potential elevation of stream nutrient concentrations in the absence of uptake. Our calculations of egg inputs using the decomposition data reflect the daily timing but not the absolute magnitude of daily inputs of mineralised nutrients due to uptake during the experiment. Stream nutrient concentrations that are below the expected elevation due to inputs probably indicate nutrient uptake.

To estimate the number of carcasses in the stream, carcasses were counted daily in two reaches (each 100 m long) during the spawning migration. Estimates of total carcass inputs were obtained by extrapolating carcass densities to the entire stream length (10.3 km). Nutrient input from these carcasses was estimated by combining total carcass inputs with measured nutrient content of whole longnose suckers that were frozen, homogenised, freeze-dried and ground into a fine powder.

To determine whether nutrients limited algal growth in Lily Bay Creek during spring 2013, we deployed nutrient-diffusing substrates following standard methods (Tank, Bernot & Rosi-Marshall, 2007). Plastic cups were filled with agar gel amended with four nutrient treatments ($n = 6$ per treatment): no added nutrients, N (0.5 M NH_4Cl), P (0.5 M KH_2PO_4) or N + P (0.5 M NH_4Cl + 0.5 M KH_2PO_4). Each cup was capped with a fritted glass disc and deployed from 16 April to 6 May 2013. After collection, glass discs were kept frozen in darkness until extraction of chlorophyll *a* in a 90% buffered ethanol (24 h, 20 °C). Extracts were analysed using fluorometry, with an acidification step. We evaluated the effect of N and P amendments on chlorophyll *a* concentration using a 2-way ANOVA.

Results

A total of 11 352 longnose suckers, 71 white suckers and 18 steelhead (*Oncorhynchus mykiss*) were captured migrating into Lily Bay Creek between 15 April and 18 May 2013. Total length was measured on 3505 longnose suckers. Sucker spawning was observed throughout the stream from the first riffle up to 10 km upstream. Individual males and females stayed in the stream for an average of 14 and 10 days, respectively, with early-arriving fish remaining longer than later migrants. All nutrient-related calculations refer exclusively to longnose suckers.

Sucker excretion was a substantial N input, constituting close to half of total sucker-derived N contributions, but it contributed little P (Fig. 1). Excretion rates (μg nutrient min^{-1}) were positively related to temperature (°C) and fish length (cm) for both NH_4 ($r^2 = 0.65$, $P < 0.001$, $\log_{10}[NH_4$ Excretion$] = 1.37*\log_{10}[$Temp$] + 1.5*\log_{10}[$Length$] - 1.88$) and SRP ($r^2 = 0.42$, $P < 0.001$, $\log_{10}[$SRP Excretion$] = 0.16*\log_{10}[$Temp$] + 2.23*\log_{10}[$Length$] - 2.73$). We estimate that longnose suckers excreted a total of 31.6 (95% CI: 23.3–43.2) kg NH_4-N and 1.0 (95% CI: 0.9–1.1) kg PO_4-P during the migration in Lily Bay Creek in 2013.

Eggs were the largest input pathway for both N and P (Fig. 1), containing 45.0 ± 0.4 (95% CI) kg N and 4.7 ± 0.1 kg P. Ovary mass was a power function of total length ($r^2 = 0.80$, $P < 0.001$, Appendix S1, Figure S1). Females contained an average of 171 g (wet mass) of eggs and collectively deposited an estimated 1161 ± 9 kg (wet mass) of eggs. Egg dry mass was $36.3 \pm 0.3\%$ (mean $\pm$ SE) of egg wet mass; $10.7 \pm 0.1\%$ of egg dry mass was N and $1.1 \pm 0.1\%$ was P.

Eggs greatly increased nutrient concentrations during decomposition in the microcosm experiment (Fig. 2). SRP increased dramatically on the fifth day and
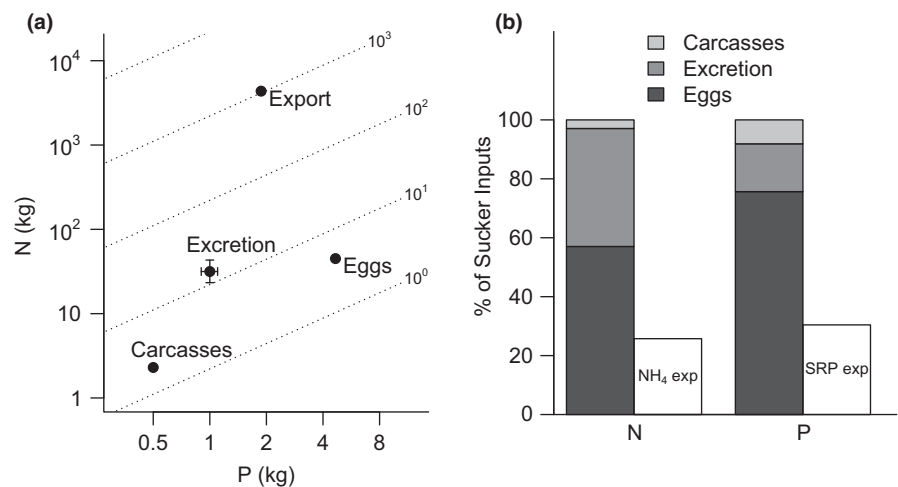
Fig. 1 (a) Magnitude of N and P inputs from sucker eggs, excretion and carcasses and total inorganic N and P export during the study. Error bars (for eggs and excretion only) show 95% confidence intervals. Dotted lines show N : P. Note that both axes are on a $\log_{10}$ scale. (b) The relative contribution each sucker pathway to total inputs. Stream export of NH_4 and SRP are shown as a proportion of sucker inputs. Sucker inputs totalled <2% of NO_3 export during the study.
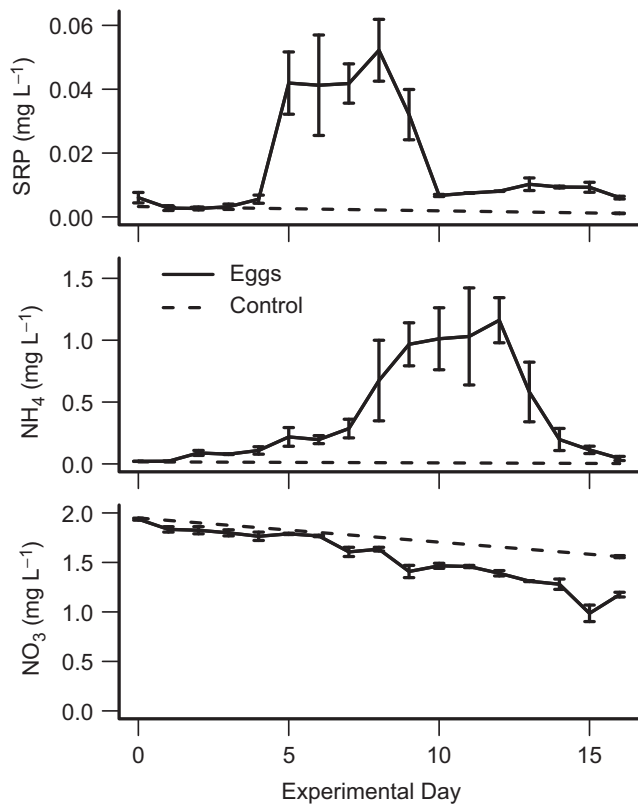
Fig. 2 Nutrient dynamics during egg decomposition in microcosms. Error bars represent ±1 SE.

subsequently decreased as algae bloomed in the microcosms. NH_4 increased more gradually, peaking on the 12th day. Eggs did not produce measurable NO_3 relative to high background concentrations. Instead, NO_3 decreased over the course of the experiment in both control and egg microcosms, but rates of decrease were much faster in the presence of eggs (951 μg L^{-1} versus 391 μg L^{-1} total decrease). The rate of NO_3 consumption rose after SRP was released in egg microcosms (Fig. 2). Estimates of inorganic nutrients released from the eggs reflected only 4.9% of N and 2.3% of P contained in the eggs.

Carcass inputs were small relative to eggs and excretion (Fig. 1). A total of two sucker carcasses were found in daily searches of two 100 m reaches during the migration, and each remained submerged in the reach for <24 h. Extrapolating the observed carcass density to the entire stream length yielded a total estimate of 103 carcasses potentially decaying in the stream during the 2013 migration. This may be an overestimate based on our one-time carcass counts over the entire stream length in 2012, which indicated over 300 carcasses along the stream banks but only 31 in the stream (E. S. Childress, unpubl. data). Many fish died during the migration, but most were either removed by fishermen (there are no harvest limits on suckers) or removed from the water by predators and scavengers. Post-spawning, whole longnose suckers were 10.4 ± 0.4% N (mean ± SE) and 2.2 ± 0.1% P by dry mass, and we assumed dry weight was 29% of wet weight based on the literature (Cummins & Wuycheck, 1971). Thus, the average fish (741 g wet mass) contained 22 g of N and 5 g of P. Assuming that 103 carcasses decomposed completely in the stream, which serves as an upper limit for carcass nutrient inputs, 2.3 kg of N and 0.5 kg of P would have been added to the stream.

Dissolved nutrient export for the 66-day sampling period was 4524 kg inorganic N and 1.9 kg SRP. The pool of dissolved inorganic N consisted of 99.5% NO_3. The dynamics of NO_3 concentration were closely related to discharge but unrelated to sucker dynamics. In contrast, NH_4 concentration dynamics were closely tied to suckers, and distinct peaks of NH_4 corresponded to the expected timing of inputs from excretion and eggs (Fig. 3a). SRP concentrations were very low throughout the study period; SRP dynamics were somewhat related to discharge and not clearly tied to suckers (Fig. 3b). Estimated daily sucker inputs exceeded or equalled daily export of NH_4 and SRP during the migration. The timing of estimated mineralisation of egg nutrients extended well beyond the time when spawning adults were present to excrete nutrients (Fig. 3).

Aggregate N inputs from longnose suckers were large relative to catchment export of NH_4 during the migration, but were small relative to NO_3 export (Fig. 1). NH_4 excretion alone was slightly larger than the observed NH_4 export, and eggs could supply an additional 220% of the NH_4 exported. However, these pathways plus carcasses still represent < 2% of the total DIN export due to the high concentrations of NO_3. For P, excreted SRP was about half of the observed SRP export, and eggs were equivalent to 248% of SRP export.

The nutrient-diffusing substrates demonstrated that algal growth was P-limited in the stream. Algal biomass accrued nearly twice as fast on substrates amended with P as on controls (Fig. 4). A 2-way ANOVA showed a significant effect of P ($F_{1,20} = 61.66$, $P < 0.001$) but not N ($F_{1,20} = 1.53$, $P = 0.23$) or N-P interaction ($F_{1,20} = 0.01$, $P = 0.92$).

Discussion

The delivery of large quantities of nutrients during the reproductive migration of iteroparous suckers demonstrates that carcass inputs are not necessary for fish to

(a)

(b)

Stream Concentration
Excretion
Eggs

(c)

Suckers
Temp

1–Apr–13   26–Apr–13   21–May–13
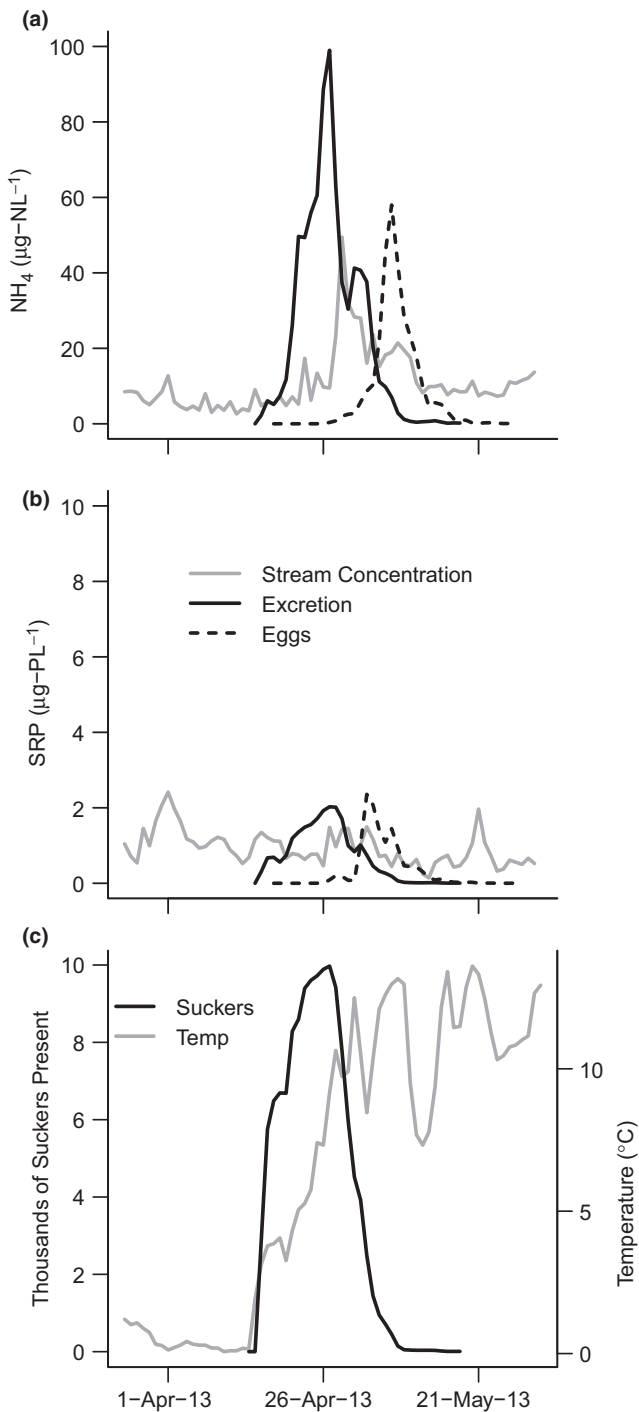
Fig. 3 (a, b) In-stream nutrient dynamics and modelled sucker excretion and egg inputs for Lily Bay Creek in 2013. Excretion and egg inputs were converted to concentration by dividing daily estimates by daily discharge, which represent a theoretical increase above background in the absence of nutrient uptake. Note that egg inputs reflect the timing but not the magnitude of inputs. (c) Dynamics of the sucker migration and average daily stream temperature.

deliver important nutrient subsidies to spawning grounds. Rather, decay of gametes and recycling of wastes by live fish are sufficient to generate ecologically
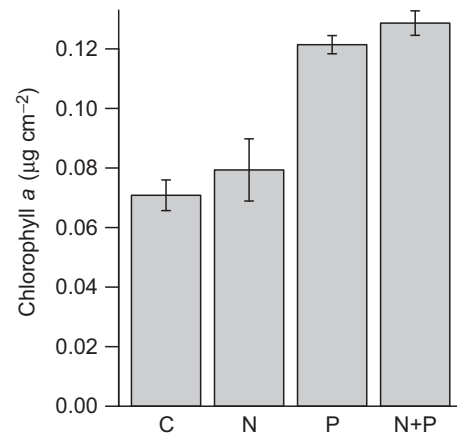
Fig. 4 Results of a nutrient-diffusing substrate experiment for substrates amended with no nutrients (C), nitrogen (N), phosphorus (P) or nitrogen and phosphorus (N + P). Error bars represent ±1 SE.

significant subsidies. As quantification of nutrient subsidies from migratory fish is expanded to account for recycling, gametes and carcasses simultaneously, the role of behaviour and life history in determining the predominant input pathways may offer opportunities to generalise across species. Recognition of these alternative input pathways also raises interesting questions about their relative accessibility to the food web (Vanni, Boros & McIntyre, 2013) and about the community and landscape contexts for interpreting the importance of subsidies (Bauer & Hoye, 2014).

Our results corroborate the general view that fish excretion can be an important nutrient flux in aquatic ecosystems (Schindler, Knapp & Leavitt, 2001; Vanni, 2002; McIntyre *et al.*, 2008; Vanni *et al.*, 2013). Ammonium dynamics reflected excretion, and excreted P appeared to be retained by the ecosystem rather than being exported. Longnose sucker excretion rates were typical for like-sized freshwater fish incubated at similar temperatures (Hall *et al.*, 2007; M. J. Vanni and P. B. McIntyre, unpubl. data), suggesting that any handling stress arising from our short-term incubations (Whiles *et al.*, 2009) or nutrient uptake in the unfiltered incubation water did not substantially affect our excretion rate estimates. In Pacific salmon, which have large carcass inputs, dissolved nutrient patterns are linked to live fish densities, suggesting that excretion is the major driver (Levi *et al.*, 2011; Tiegs *et al.*, 2011). However, the ecological importance of excretion will depend on the number of fish, their size and their residence time in the ecosystem. For example, population-level excretion rates were high for an anadromous alewife migration, but total inputs were low because these fish

stayed in the streams for only 2 h (Walters, Barnes & Post, 2009).

Gametes have received little attention as a nutrient subsidy, but we found that they represent a major nutrient flux during sucker migrations. Eggs are directly available to consumers and represent a food resource rich in both nutrients and energy. Although the gametes are available only for a short period, they can provide substantial portions of consumers' annual energy budgets. During salmon migrations, resident fish rely heavily on salmon eggs as a food resource (Koshino, Kudo & Kaeriyama, 2013), which can support most of their annual growth (Bentley *et al.*, 2012; Stockwell *et al.*, 2014). Sucker eggs can also constitute most of resident trout diets during the migration (E. S. Childress, personal observation). Additionally, lake whitefish will follow sucker migrations into large rivers, where they feed almost exclusively on sucker eggs during the migration (Dion & Whoriskey, 1992).

In addition to direct availability of eggs, the release of nutrients during decomposition makes them available for uptake by primary producers and microbes. The release of nutrients from eggs appears to extend the duration of the subsidy beyond the time when spawning adults are present in the stream. In the decomposition experiment, only a small proportion of the nutrients contained in the eggs were represented in the increases in inorganic nutrients. The rapid drawdown in NH_4 and SRP concentrations after initial increases and the continuous decline in NO_3 concentrations indicate rapid uptake in the microcosms. Because uptake and release occurred simultaneously, the observed increases in nutrient concentrations do not reflect the total nutrients released during decomposition. Additionally, some egg nutrients may be converted directly to microbial and fungal biomass during decomposition or broken down into organic constituents. To sidestep the complexities of interpreting nutrient data from the microcosm experiment, we used total nutrient inputs from the eggs as the basis for comparisons with other inputs within a mass balance framework. While conditions in the microcosms and the stream were quite different, uptake in microcosms and lower stream concentrations than expected based on inputs suggest that egg decomposition may be associated with rapid nutrient uptake.

Fish eggs have the potential to be an important nutrient flux in aquatic ecosystems more broadly. Although eggs are recognised as an important energy source (Bentley *et al.*, 2012; Stockwell *et al.*, 2014), they have received less attention from a nutrient perspective (but

see Gende *et al.*, 2004). Fish can be a major nutrient stock in lakes and streams (e.g. Carpenter *et al.*, 1992; Vanni *et al.*, 2013), and females often deposit large proportions of their body mass as eggs (Moyle & Cech, 2004). Because fish egg survival rates are low (Dahlberg, 1979), each spawning bout is a pulsed release of substantial quantities of nutrients sequestered from the diet over relatively long periods of time.

Although carcasses are a major nutrient source from migrations of semelparous fish (Naiman *et al.*, 2002), they were of little importance as a nutrient source during the sucker migration. Sucker carcasses rarely remain in small streams for more than a few days before being removed. Streamside camera traps elsewhere in our study region showed that carcasses are efficiently removed from streams by scavenging birds and mammals (P. B. McIntyre, unpubl. data), which supports our observation that there are few carcasses in the stream but a larger number that are partially or mostly consumed upon the banks. Thus, it appears that sucker carcasses may be more important as a subsidy to terrestrial predators and scavengers than for stream nutrient budgets and biota.

The nutrients delivered by suckers are likely to be ecologically important in this system. Algal accrual was strongly P-limited, and estimated P inputs from suckers were much larger than the inorganic P export during the study. Assuming that average daily export during our sampling period is representative of the rest of the year, estimated sucker inputs during the 2-month breeding season would be equivalent to 59% of annual inorganic P export but only 0.3% of annual DIN export. This rough comparison is likely to be conservative because our study period encompasses the highest period of sustained discharge in the annual hydrograph (i.e. spring snowmelt) and nutrient concentrations are positively related to discharge, so nutrient export is likely to be lower during the rest of the year. Additionally, some of the exported P during our study was probably sucker-derived, thereby elevating the ratio of inputs from fish to background P export from the catchment. Thus, we conclude that the P contributions by longnose suckers are almost certainly a significant portion of the annual budget. Our experiment with nutrient-diffusing substrates indicates that this P subsidy is likely to increase algal productivity, and thereby benefit the broader food web (Naiman *et al.*, 2002; Reichert, Greene & Bilby, 2008; Childress *et al.*, 2014).

The use of fish-derived nutrients through ecosystem uptake will ultimately determine their ecological

importance. Uptake may mask the increased nutrient concentrations expected from subsidies, particularly when uptake rates are high relative to the available pool. The combination of P-limited algal accrual and consistently low P concentrations suggests that sucker-derived P was in high demand in Lily Bay Creek. In contrast, nitrogen concentrations showed a clear signal of inputs from suckers only as NH_4. Interestingly, the lack of enhanced NH_4 concentrations in the first week after fish arrived suggests that ecosystem N demand was sufficient to consume all excreted N initially despite high background NO_3. Only later in the migration period did excretion apparently saturate the demand for NH_4, leading to enhanced concentrations of NH_4 leaving the system.

Given the large proportion of agriculture in the catchment, sucker P inputs were remarkably large relative to inorganic export. High NO_3 concentrations (up to 3.4 mg L^{-1}) were likely driven primarily by agricultural inputs (Allan, Erickson & Fay, 1997; Carpenter *et al.*, 1998) with some additional contribution of atmospheric deposition (Han & Allan, 2012). P remained very low in spite of the agricultural influence, which is consistent with higher retention of anthropogenic P than N in Lake Michigan catchments (Han, Bosch & Allan, 2011). The importance of nutrient transport by migratory species is often presumed to be limited to less developed areas and oligotrophic systems (Flecker *et al.*, 2010). However, our results demonstrate that migratory fish can contribute ecologically relevant quantities of phosphorus even in areas with 70% agricultural land use.

Although P was limiting in our study system due to agricultural inputs of N, more remote streams with large sucker migrations can be N-limited (P. B. McIntyre, unpubl. data). Because the N : P of excretion was much higher than that of eggs, both excretion and eggs are likely to be important in N-limited systems, while eggs are of primary importance in P-limited systems. Thus, the nutrient stoichiometry of inputs from fish and the environmental context of nutrient limitation will jointly determine the relative importance of particular nutrient input pathways.

Longnose suckers are not exceptional in their excretion rates (Hall *et al.*, 2007) or ovary mass (Moyle & Cech, 2004) given their body size, suggesting that the egg and excretion inputs we have documented may be representative of large migrations of medium-sized fish in rivers elsewhere. Since the majority of migratory fish worldwide are iteroparous (Flecker *et al.*, 2010), both the excretion and egg pathways are likely to be important nutrient sources in most cases. Many fish migrations – including some sucker species (Cooke *et al.*, 2005) – have been greatly reduced (Humphries & Winemiller, 2009; Limburg & Waldman, 2009), so the persistence of large migrations of longnose and white suckers across much of North America suggests that these species are exceptionally resilient. As such, our results may provide some perspective on the past ecological significance of large fish migrations that are now gone, and thus further impetus for the conservation and restoration of fish migrations in general.

Our results contribute to an expanding the literature on the importance of animal excretion for nutrient cycling in aquatic ecosystems and suggest that egg contributions can also represent a major nutrient flux. Mass mortality is not requisite for important nutrient subsidies from fish migrations. Recognition of these multiple pathways and their differing availability to food-web components is critical for determining the magnitude of nutrients delivered by fish and the mechanisms by which ecosystems respond.

More broadly, animal breeding aggregations concentrate biomass and are often important sources of nutrients and energy, whether through excretion, gamete deposition or mortality. Many animals cross habitat and ecosystem boundaries during reproductive movements, making these periods hot moments of cross-ecosystem subsidies. In addition to fish migrations, many amphibians, turtles and aquatic insects move across ecosystem boundaries to reproduce. For instance, amphibian egg deposition can be a large nutrient source for breeding ponds (Regester & Whiles, 2006), and aquatic insects become an important food source for riparian insectivores as they emerge to reproduce (Nakano & Murakami, 2001). Our findings highlight the importance of reproductive movements for providing nutrient subsidies and indicate that migrations of iteroparous fish can deliver large quantities of nutrients to their spawning grounds.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Estimation of nutrient inputs from sucker eggs.

Figure S1. Relationship between total length and ovary mass among female longnose suckers.

Figure S2. Frequency histogram of total length for female longnose suckers captured in Lily Bay Creek during 2013 as they arrived to spawn.

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