Cross-Ecosystem Delivery of Nutrients to Streams:

The Role of Fish Migrations and Landscape Processes

By

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Abstract

Movement of nutrients among ecosystems is a key process that drives productivity and influences ecological dynamics. This dissertation explores two aspects of nutrient transfer among ecosystems: translocation by migratory species and landscape controls on terrestrial ecosystem losses. As migrants move among ecosystems they can transfer materials and energy that alter ecosystem dynamics and processes. Among fishes, salmon are well-known to transfer large quantities of nutrients from the ocean to their freshwater spawning grounds as they migrate and die en masse. Less is known about the role of fish that spawn multiple times over their life and thus do not leave large quantities of carcasses in their spawning grounds. Much of this dissertation explores the role of white and longnose suckers as nutrient vectors in Great Lakes tributaries.

I documented the early life history of longnose suckers, pathways of nutrient contributions from sucker migrations, and ecosystem metabolic responses. I found that sucker eggs and excretion contribute large quantities of nutrients to their spawning streams. Because early life mortality is often >99% and larvae spend little time feeding in their spawning streams, most of these nutrients become available to stream biota. Sucker nutrient contributions were large relative to background availability, even in an agricultural watershed context, and they led to increased gross primary production but not ecosystem respiration.

Landscape processes also exert important influence over the availability and transport of nutrients in streams. Human land use has transformed many stream ecosystems as agriculture and urban development supply nutrients and alter stream hydrology. In the Hawaiian archipelago, human land use overlays large gradients of substrate age, precipitation, and slope which are important determinants of nutrient availability in terrestrial ecosystems. I examined the relative importance of natural gradients and human land use in determining stream nutrient concentrations and found that weathering patterns remain the primary control over P availability across the landscape, but that human activities are more important for N.

Introduction

Movement of nutrients across landscapes and ecosystems regulates ecosystem function and community structure (Polis et al. 1997). Streams are tightly linked with surrounding ecosystems through the delivery of nutrients and organic matter from the landscape, exchanges with floodplains, allochthonous inputs from riparian vegetation, and hyporheic exchange (Lamberti et al. 2010). Nutrient availability is controlled by a suite of processes ranging in scale from in-stream cycling to regional and global atmospheric processes that ultimately influence species diversity and composition. In fluvial ecosystems, processes generally operate with the force of gravity, as water flows over and through the landscape interacting with soils, geology, and organisms. In contrast, mechanisms that deliver materials against the current can be important for maintaining productivity. In this dissertation, I examine the delivery of nutrients to stream ecosystems: upstream through the movements of migratory fish and downstream through control by landscape processes.

Upstream nutrient delivery by migratory fish

Animals can be important nutrient and energy vectors as they move among habitats to feed and reproduce, supplying nutrients via waste products, gametes, and mortality. Each of these pathways can be important for supporting productivity and influencing ecological dynamics. For example, sea birds deposit nutrient-rich guano in roosting habitats after feeding on ocean life, which supports productivity on oceanic islands (Anderson and Polis 1999). Amphibians supply nutrients to vernal pools through egg deposition (Regester et al. 2006).

Emergent aquatic insects subsidize terrestrial consumers and plants (Hoekman et al. 2012, Bultman et al. 2014). The role that particular species play in transferring materials is dictated by their life history and behavioral characteristics as well as environmental context.

Our knowledge of nutrient subsidies from fish migrations is based almost exclusively on Pacific salmon, and the influence of salmon nutrients has been a longstanding focus of ecological research (Juday et al. 1932, Janetski et al. 2009). Salmon achieve most of their growth in the ocean but migrate into rivers to spawn, and most species are semelparous, dying in the stream after spawning once. Marine-derived nutrients delivered by migrating salmon are incorporated into all trophic levels in streams and riparian zones.

Although salmon are a fascinating model for the study of fish migrations, their life history and behavior are unusual among migratory species worldwide. Most Pacific salmon are semelparous, whereas most migratory fish species spawn many times during their life (Flecker et al. 2010). The large substrate disturbance caused by salmon is also not typical of migratory species, because many are broadcast spawners and do not disturb the substrate during spawning (Page and Johnston 1990, Walters et al. 2009). As such, it is important to understand how other fishes that do not die en masse or do not disturb the substrate influence the ecology of their spawning grounds. In my previous work, I found that iteroparous migrations of suckers in Great Lakes tributaries can deliver nutrients and spur productivity of algae and insects (Childress et al. 2014). I build on this work by examining the pathways of nutrient delivery and the influence of nutrients on ecosystem function during migrations of white (*Catostomus catostomus*) and longnose suckers (*Catostomus catostomus*) in Great Lakes tributaries.

Longnose suckers are widespread and often abundant (Scott and Crossman 1973); however they have been largely overlooked by managers and researchers alike because they are viewed as rough or trash fish. As such, the scientific literature contains very little information about the life history and basic ecology of longnose suckers, and knowing survivorship and stream residence time is necessary for determining the net material contributions during spawning migration. In **Chapter 1**, I document the early life history of longnose suckers, evaluating fecundity, larval export, survivorship, and growth. In addition to providing a basis for determining the nutrient contributions of suckers, this work provides a foundation for understanding variability and bottlenecks of recruitment and population dynamics. Because our study sites lie near the southern edge of the range of longnose suckers, the populations may be vulnerable to declines or extirpation as environmental conditions shift with climate change (Parmesan 2006). Population responses to environmental stressors may lag behind changes in vital rates in long-lived species that rely on infrequent highly successful spawning events (Vélez-Espino et al. 2006).

The mechanism by which nutrients are delivered to the tributaries during sucker migrations is the focus of **Chapter 2**. I quantified the contributions of carcasses, gametes, and excretion during a sucker migration using direct measurements on individuals and scaling up to the population level. I put the magnitude of the sucker contributions into the context of background nutrient fluxes and nutrient limitation to help determine the ecological relevance of the inputs. Understanding the pathways by which iteroparous fish deliver nutrient subsidies is important for determining which species and under what context fish migrations will deliver nutrient subsidies because most species around the world are iteroparous, but our understanding of the role of fish migrations in delivering nutrient subsidies is primarily based on semelparous Pacific salmon.

In **Chapter 3**, I examine the influence of nutrient contributions from suckers on whole stream metabolism and nutrient concentrations in Lake Michigan tributaries. I used existing barriers created by road-stream crossings to evaluate the ecosystem metabolism and nutrient dynamics of streams with and without sucker migrations. This chapter builds on my previous work examining the ecological influence of suckers on algae and insects in a single stream to encompass a set of streams and examine responses of ecosystem function. It also provides a comparison with findings that salmon enhance ecosystem respiration and depress gross primary production due to disturbance during nest building (Holtgrieve and Schindler 2011, Levi et al. 2013). Because suckers are broadcast spawners and do not represent a significant disturbance, this study provides a test of whether this difference in spawning behavior alters the ecosystem response to fish migrations.

The first three chapters expand knowledge of the influence of fish migrations on stream ecosystems, providing a test of the generality of extensive research on the role of Pacific salmon. Because suckers differ from salmon in both life history and spawning behavior, these chapters further our understanding of how these species characteristics modulate the role of particular fishes.

Landscape delivery of nutrients

Although mobile species can move nutrients against the current, nutrients generally reach stream ecosystems as they flow down the landscape. As such, streams integrate the processes within their watersheds (Bormann and Likens 1967), and landscape history and current land use play a large role in determining the flux of nutrients through streams. Hawaii offers a rare diversity of environmental gradients to examine the influence of landscape properties on stream ecosystems. Extensive research on the biogeochemistry of Hawaii's terrestrial ecosystems has shown that age and precipitation gradients are important for determining nutrient availability and productivity (Vitousek 2004). Specifically, the weathering of young substrates provides P to new ecosystems, which is depleted over time (Hedin et al. 2003). In contrast, N is scarce on new substrates and tends to accumulate through biological fixation and atmospheric deposition (Vitousek et al. 2009). Because the Hawaiian islands were formed by volcanic activity over millions of years as the Pacific plate moved across a hotspot, there are strong gradients of age from newly formed lava flows to substrates over 4 million years old (Wilson 1963). Additionally, as the prevailing winds rise over the land and drop their moisture they create strong gradients in precipitation (Ferrier et al. 2013). These gradients create a mosaic of weathering conditions that influence nutrient availability in terrestrial ecosystems (Vitousek 2004).

Overlying these gradients of ecosystem development is large variability in land use. Urbanization has transformed substantial portions of the Hawaiian landscape, but some catchments remain virtually uninhabited. This provides an ideal setting to examine the relative importance of landscape characteristics and human land use across for nutrient availability in streams, which is the topic of **Chapter 4**. The gradients of ecosystem development are viewed as a primary control on the nutrient status of Hawaii's landscape, and the goal of this chapter is to determine whether that paradigm holds in the context of an increasingly human dominated landscape.

As a whole this dissertation examines role of watershed context in controlling nutrient availability by mediating downslope losses and ability of fishes transport materials upstream against the flow. Because streams are intimately linked with the surrounding ecosystems, such perspectives on the interactions between streams and their surroundings are essential for understanding dynamics and processes in streams. This dissertation builds on and combines paradigms for these interactions. The fish migration research broadens our understanding of the role of fish migrations, shifting the paradigm from a focus on semelparous Pacific salmon in oligotrophic streams to one that incorporates variability in life history, behavior, and watershed context. Similarly, Chapter 4 combines paradigms of nutrient control by ecosystem development and human land use, which are both prominent but have been surprisingly separate in the literature. This yields a new perspective on the interactions between types of landscape variation.

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Chapter 1

Reproductive success and early life history of longnose suckers in Great Lakes tributaries

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Abstract

Mortality during the egg and larval stages can be major determinants of year-class strength and population dynamics in fishes. Although, the longnose sucker (*Catostomus catostomus*) is among the most widespread fish in North America, little is known about its early life history. We examined fecundity and early life survivorship during sucker spawning events in three small Lake Michigan tributaries. Although the number of eggs deposited was similar in each case, larval export varied by over four orders of magnitude from around 1,000 to over 18 million. Environmental conditions varied strongly across the years, suggesting that spring flow and temperature are important determinants of egg success. Based on otolith ages of larvae, most individuals that survived to outmigration hatched on two days, although spawning lasted for around 10 days. Larvae typically spent less than two weeks in the stream and emigrated around the time of transition from endogenous to exogenous feeding before substantial growth occurred. In two of three cases, larvae drifted exclusively at night consistent with previous findings. However, in the year when larvae were very abundant, high drift rates occurred during the day and at night, suggesting that high densities may overwhelm available habitat or reduce predation risk. Our results indicate that survival in tributary streams from egg deposition to larval export is

highly variable in longnose suckers. These large differences in early life survival are likely to translate to variability in recruitment and influence population structure and dynamics.

Introduction

Mortality during early life stages is a major driver of fish population dynamics (Fogarty et al. 1991). Fish eggs and larvae are particularly sensitive to abiotic conditions (Mion et al. 1998) and vulnerable to predation (Almany and Webster 2005), which often leads to high mortality rates (Dahlberg 1979). Interannual variability in success during the egg and larval stages can determine year-class strength (Houde 1989, Bailey et al. 2012), so determining variability in early mortality is critical for understanding the drivers of recruitment and population dynamics (Chambers and Trippel 1997).

Populations of suckers (Catostomidae) are major components of aquatic ecosystems across North America (Cooke et al. 2005). Suckers serve an important food web role as prey for a wide variety of animals, including bald eagles (Hoff et al. 2004), otters (Wengeler et al. 2010), and valuable game fish such as walleye and northern pike (Beaudoin et al. 1999, Bertolo and Magnan 2005). Additionally, many suckers are efficient benthic invertivores and can exert top-down control on invertebrate populations (Hayes et al. 1992). Variability in larval production could play an important role in these food web interactions. Further, many sucker species are imperiled, particularly in Western North America, and understanding population bottlenecks is important for species conservation (Cooke et al. 2005). Finally, suckers serve an important ecological role as vectors of nutrients and energy during their spawning migrations (Chapter 2), which support productivity in their spawning grounds (Childress et al. 2014). Thus, determining egg and larval mortality as well as residence time in streams is important for understanding the net contributions of materials from sucker migrations. This range of ecological roles makes suckers an important component of the ecology of freshwater ecosystems.

Longnose suckers (*Catostomus catostomus*) are distributed throughout northern North America and are one of two sucker species native to Asia (Scott and Crossman 1973). In spite of their broad distribution, most details of their ecology are poorly documented. Longnose suckers are long-lived with low adult mortality rates (Bailey 1969), and early life history could be an important driver of recruitment and population dynamics (Vélez-Espino et al. 2006). However, typical rates of recruitment success have not been quantified. In this study, we analyze the fecundity and early life history of longnose suckers in small tributaries of Lake Michigan. We present data on the size and phenology of adult spawning migrations, the relationship between female size and fecundity, larval residence time and growth in the stream, diel and seasonal larval drift patterns, and rates of survival between egg deposition and larval outmigration.

Methods

Studies on the early life history of longnose suckers were conducted on three tributaries to northwestern Lake Michigan: Wilsey Bay Creek in 2009 (45.7035 N, 86.9335 W), Hibbard Creek (44.9877 N, 87.1760 W) in 2012, and Lily Bay Creek (44.8476 N, 87.2684 W) in 2013. All three are low-gradient, second-order streams with sand and silt substrates in pools between riffles with gravel and cobble substrates. The riparian vegetation at each site includes a mix of grasses, cedars, and alders. Discharge is strongly seasonal, rising as the snow pack melts and falling throughout the late spring and summer. The Great Lakes lie near the southern edge of the longnose sucker distribution and the northern edge of the distribution of white suckers (*Catostomus commersonii*) (Scott and Crossman 1973), and all study streams receive migrations of ~10,000 suckers in April-May, including both longnose and white suckers. Hibbard and Lily Bay Creeks are dominated by longnose suckers, while Wilsey Bay Creek has equal numbers of the two species.

To determine the timing, number, size, and sex of spawning suckers, trap nets were deployed during the migration. In Wilsey Bay and Lily Bay Creeks, two nets spanning the entire stream were deployed back-to-back: one faced downstream and caught fish migrating upstream, and the other faced upstream and caught fish leaving the stream. Nets were installed just after the initiation of the migration, and all incoming fish were marked with a dorsal fin clip to enable identification of fish that entered the stream prior to net installation. In Hibbard Creek, a single trap net spanning 80% of the stream width was deployed facing upstream but captured both in- and out-migrating fish. All incoming fish were marked with a dorsal fin clip, and population size was estimated using recapture rates of marked fish with the assumption that capture probabilities were equal for marked and unmarked fish during outmigration. In all cases, fish were released daily after determination of species and sex for all individuals and measuring total length on a large subset (n = 11,359 of 28,868 fish). Wet mass was measured for a smaller subset of individuals (n = 507).

To estimate fecundity and total egg deposition, ovaries were analyzed from 41 females collected in Hibbard Creek and Lily Bay Creek. Ovaries were obtained by dissecting newly arrived females after obtaining mass and total length measurements. Extracted ovaries were weighed immediately and then stored frozen. Ovaries were gravimetrically subsampled (n = 5 per ovary; 1.0 ± 0.2 g), and eggs were counted to determine the mean mass per egg (Bagenal and Braum 1978). Total fecundity was estimated by dividing total ovary mass by mean egg mass. We found that ovaries lost around 3% of their mass to sublimation while frozen, so fecundity estimates were based on ovary mass measured after storage. To estimate population-level egg deposition, we used linear regression of fecundity against fish mass to predict fecundity for every female. Mass was predicted from a power-function relationship between length and mass for females with a length measurement and fish without size measurements were assigned the average fecundity. A similar approach was used to estimate white sucker fecundity and egg deposition in Wilsey Bay Creek in 2009 (Hui-Yu Wang and P. McIntyre, unpublished data). Based on the observation that large numbers of females began emigrating the day after spawning was first observed, the timing of egg deposition was estimated by assuming that females deposited their eggs the day prior to emigration.

Egg density on the stream benthos was measured using daily benthic samples in the most downstream riffle in Lily Bay Creek in 2013. A Hess sampler (856 cm^2, 500 μm) was placed at random within a 30m sampling reach such that specific locations were not resampled. The substrate was disturbed to a depth of 5 cm for 30 seconds. Two samples were taken each day from 5 May 2013 to 22 May 2013. Samples were preserved in 70% ethanol, and eggs were counted in the laboratory under a dissecting microscope with 12x magnification.

To estimate total larval export, the rate of larval drift was measured daily throughout the emigration period using drift nets (363μm, 45.7 x 30.5 cm). In 2013, when the drifting season was much longer than in other years, sampling was less frequent in the late season when fewer larvae were drifting. To account for variation in larval drift by time of day, we conducted intensive diel sampling at each site for 1-2 days near the peak of emigration. This enabled extrapolation of each daily sample to estimate total daily export. Previous studies (Geen et al. 1966, Clifford 1972) and our own pilot sampling suggested that larvae would not drift during the day, so sampling was conducted for 12 hours overnight in 2009. However, full 24-hour sampling was conducted in 2012 and 2013. Daily samples were targeted to overlap with high drift periods and maximize catch probability. Because diel patterns varied among years, sampling times also varied (see Results, Fig. 3); samples were collected at night in 2009 and 2012 and during the day in 2013. At least two samples were collected on each day. Larvae were identified as catostomids (Auer 1982), but no morphological characteristics can differentiate between young white and longnose sucker larvae (Snyder et al. 2004) so we must assume that both species were represented in the drift in proportion to the number of adults spawning.

Length of drift net sets varied across sampling years due to stream conditions and larval densities. In 2009 and 2012 nets were set for 15 min, but times were shortened to 2 min in 2013 to reduce clogging by high densities of larvae. The volume of water sampled by the drift nets was calculated by measuring flow entering the nets and multiplying by the sample duration and net dimensions. In each year, daily water level measurements were used to estimate discharge from a power-function relationship between water level and discharge (n = 7-12 observations per stream; all $R^2 > 0.95$). Daily larval export was estimated using the ratio of stream discharge to volume sampled and the ratio of total export during the diel sampling to larvae caught at the sampling time using the following equation:

$$Daily\ export = \#\ Caught * \frac{Stream\ discharge}{Volume\ sampled} * \frac{Diel\ export}{Export\ at\ sample\ time}$$

Error in the daily estimates was calculated using the variability in estimates based on replicate samples. In 2013, larval export was estimated on days without direct measurement using linear interpolation.

Larval age at emigration and hatch dates were measured for larvae in Lily Bay Creek in 2013. Because larvae were very abundant and >99% of spawning fish were longnose suckers, we had high confidence that catostomid larvae were longnose suckers. Larval age was estimated by counting daily growth rings in otoliths (Hoff et al. 1997) from 30 individuals chosen at random from samples representing the full range of capture dates. Otoliths were removed from ethanol-preserved larvae and mounted on glass slides with clear Crystalbond^{TM} adhesive (Secor et al. 1992). The small size of the otoliths made daily rings visible without sectioning or polishing. Lapillar and sagittal otoliths have both been demonstrated to form daily rings in catostomids beginning on the hatch day (Hoff et al. 1997). Sagittal otoliths were slightly larger than lapillae; however their morphology changed at around 20 days of age, and the development of rostra obscured daily rings. Thus, lapillar otoliths were used to estimate age. All otoliths were aged by two researchers, and the average of the age estimates was used for analysis. Age estimates were used to back calculate the day of hatch by subtracting age from the capture date.

Larval size was measured over the range of emigration dates in 2009 ($n = 580$) and 2013 ($n = 159$). Total length was measured on digital photographs taken under a microscope (10x magnification) using ImageJ software (Schneider et al. 2012). All larvae used in size measurements were captured in drift samples with the exception of larvae from Lily Bay Creek on 11 July 2013. On that date, no larvae were captured in drift samples but some were still present in the pool, so a dip-net was used to sample larvae for size measurements.

Results

Total numbers of migrating suckers were similar among the spawning events; however, the ratio of white to longnose suckers varied. Wilsey Bay Creek had similar numbers of white and longnose suckers, whereas Lily Bay Creek and Hibbard Creek were dominated by longnose suckers (Table 1). Female longnose suckers were consistently larger than males (Fig. 1), and Wilsey Bay Creek had larger average body size for both sexes than the other two sites.

Additionally, fish migrating into Wilsey Bay Creek showed a bimodal size distribution for both males and females, while the other two populations were unimodal. Sex ratios were all biased towards females (Wilsey Bay Creek: 86% female; Hibbard Creek: 68%; Lily Bay Creek: 69%).

Longnose sucker fecundity averaged 30,580 eggs and was positively related to mass ($R^2 = 0.83$, $P > 0.001$; Fecundity = 36.52*Mass (g) – 6612.5; Fig. 2). White sucker fecundity averaged 30,778 per female and was also correlated with mass ($R^2 = 0.67$, $P < 0.001$; Fecundity = 22.41*Mass(g) + 6294.3). Total estimated egg deposition was similar among spawning events with 1.8×10^6 in Wilsey Bay Creek in 2009, 2.4×10^6 in Hibbard Creek in 2012, and 2.1×10^6 in Lily Bay Creek in 2013.

Diel larval sampling showed nocturnal peaks in larval drift for all three spawning events, although the timing of the peak differed among streams (Fig. 3). Drift was observed exclusively during the night in 2012, whereas most of the larvae drifted during the daytime in 2013 when densities were much higher (Fig. 3). Although larvae were captured in all diel samples in 2013, there was a distinct diel pattern with fewer larvae drifting at dawn and dusk.

Despite similar numbers of spawners and eggs deposited in each spawning event, estimated annual larval export varied 20,000-fold (Table 1). Larval export was highest in Lily Bay Creek in 2013, and large numbers of larvae were drifting when our sampling began, such that total export was likely underestimated. At all three sites, a large majority of larvae emigrated during a much narrower time window than the period of adult spawning. More than 90% of all larvae emigrated over eight-day periods in 2009 and 2012, and 77% of larvae emigrated in the first eight days of sampling in 2013 despite the fact that emigrating larvae were observed for 50 days.

Larval age estimates were precise overall with an average coefficient of variation of 3% between readers, but estimates became less precise as larval age increased. Average difference in age estimates between readers were grouped in 10 day age increments and differed by 0.33 days in larvae younger than 15 days old (i.e., 2% deviation) and < 2 days in larvae < 45 days old (5% deviation), but agreement decreased to an average difference of 4.2 days in larvae >45 days old (10% deviation). Although precision was lower for older larvae, all but one of the back calculated hatch dates for larvae >45 days old overlapped with hatch dates of younger larvae. Back calculation of hatch dates showed that emigrating larvae all hatched within a six-day window in Lily Bay Creek in 2013, despite the fact that we aged larvae collected over a 52 day period. In fact, 83% of aged larvae hatched on 2 consecutive days (Fig. 4). Egg density on the benthos decreased dramatically coincident with the hatching.

Average egg incubation time in Lily Bay Creek in 2013, estimated as the difference between peak egg deposition and peak hatching, was 12 days (Fig. 4). Most larvae emigrated 9-14 days after hatching, but a small subset remained in the stream during the postlarval period for over 50 days. After most individuals had emigrated, larvae were present in the very slow, deep pool just upstream of the mouth, but no larvae were observed upstream in reaches with faster flowing water.

Most larvae did not achieve substantial growth during their residence in the stream, but in Lily Bay Creek in 2013 a small subset of individuals tripled in length (Fig. 5). In Wilsey Bay Creek in 2009, size did not increase substantially over the short emigration period. However, during the more protracted emigration period in Lily Bay Creek in 2013, there was clear evidence of growth in the stream. Larval dry mass (mg) was strongly related to total length (mm) ($R^2 = 0.98$, $P < 0.001$, $\text{Mass} = 2.778 \times 10^{-6} \times \text{TL}^{4.658}$, Fig. 5).

Discussion

Our results demonstrate extremely high variability in larval export among sucker spawning events of similar size. High egg mortality rates during some spawning events are likely to act as a recruitment bottleneck. Even though longnose suckers spend only a few weeks in their natal habitat, our observations indicate that stream conditions are an important determinant of annual recruitment.

Abiotic conditions such as temperature and flow during the egg incubation and larval periods frequently influence larval survival in fishes (Mion et al. 1998). Because longnose sucker larval production varied by over four orders of magnitude among spawning events with similar reproductive effort, we infer that environmental conditions during early ontogeny are likely to be responsible. In other catostomids, larval success increases with flow magnitude (Johnston et al. 1995), and coincidence of high flows with the spawning period can also increase survivorship (Bednarski et al. 2008). Our observational approach prevents direct tests of particular factors, but the spring of 2013 had high, sustained flows and gradual warming during the spawning period. In contrast, 2012 had lower flows and variable temperatures, which resulted in most eggs being deposited low in the watershed and experiencing cold temperatures during incubation. Cold temperatures that extend the incubation period often increase egg mortality (Hamel et al. 1997). Conditions in 2009 were intermediate; flows were moderate and temperature increased gradually. Although we did not sample any stream for larvae over multiple years, we looked for larvae in the backwaters of Lily Bay Creek in 2012 yet found none, whereas a single sweep of a dipnet at the same sites yielded thousands of larvae in 2013. Thus, our results are consistent with the general idea that spring flow conditions are important for early survival of catostomids

(Johnston et al. 1995, Bednarski et al. 2008, Scoppettone and Rissler 2012) and suggest that abiotic conditions can contribute to a recruitment bottleneck in longnose suckers.

In Lily Bay Creek in 2012, thousands of eggs accumulated in depositional areas in the lower reaches of the stream and decomposed. In 2013, few eggs were observed in these same depositional areas, and adults migrated over twice as far upstream into intermittent reaches only inundated in some years during spring run-off. Access to these upstream reaches may have driven the differences in larval survival. There are a few possible explanations for this. Upstream reaches may provide better spawning habitat, they may contain fewer predators because they are intermittent and fish and macroinvertebrates would be unable to persist throughout the year. Another possible explanation for the differences is temperature fluctuation.

The substantial larval drift during daylight hours in 2013 differs from previous reports of sucker drift behavior. All previous studies have found a peak in larval drift during the night and very little drift during daylight (Geen et al. 1966, Clifford 1972, Walton 1980, Modde and Muirhead 1994, Johnston et al. 1995, Johnston 1997, D’Amours et al. 2001, White and Harvey 2003). Our observations of larval drift patterns at low densities in Wilsey Bay Creek and Hibbard Creek agree with these findings; however, when larval densities were high in Lily Bay Creek, far more drift occurred during the day than at night. Catostomid larvae typically seek flow refuge in backwaters during the day (Ellsworth et al. 2010), and it is possible that daytime drift was spurred by high densities of larvae overwhelming the available refuge habitat. However, there were clear diel dynamics with drift minima at dawn and dusk, suggesting that larvae were able to remove themselves from the drift. Larval fish are reported to drift during the day in large, turbid rivers (Reeves and Galat 2010), but our study streams were small and clear with total suspended solids less than 1 mg L^{-1} during emigration.

Predation risk is one possible explanation for the interannual variability in diel drift patterns as well as the low drift rates at dawn and dusk in 2013. We observed predation on both eggs and larvae during spawning migrations. Individual rainbow trout (*Oncorhynchus mykiss*) consumed hundreds of eggs. Brook sticklebacks (*Culaea inconstans*) and predaceous diving beetle (Dytiscidae) larvae were observed feeding on sucker larvae. Shiners (*Notropis* spp.) appeared in the stream around the time of larval outmigration, and other predators, such as odonates and juvenile northern pike (*Esox lucius*), were also present in the streams. High larval densities may reduce predation risk during the day by overwhelming predators (Wrona and Dixon 1991), making diurnal drift a viable strategy. In addition, fish may be particularly vulnerable to predation at dawn and dusk because visual adaptation to light transitions is slow (Munz and McFarland 1973), and the diel dynamics that we observed in 2013 may reflect avoidance of crepuscular predators, like northern pike or trout (Reebs 2002).

The life history results from this study agree well with the limited information available for longnose suckers and with the characteristics of catostomids more generally. Our estimates of a 12-day egg incubation period agree with laboratory studies documenting incubation times between 8 and 14 days depending on temperature (Walton 1980). Additionally, many catostomids emigrate from their hatching grounds quickly after absorption of the yolk-sack, returning to the growth habitat around the time of transition from endogenous to exogenous feeding (Cooperman and Markle 2003, Ellsworth et al. 2010). In this study, most larvae achieved little growth in the stream because they emigrated shortly after the transition to exogenous feeding. Our observed female biased sex ratios are consistent with previous reports that females experience lower mortality than males (Bailey 1969). Larger female size probably reflects delayed maturity in females relative to males to maximize reproductive output (Grabowski et al. 2012; E. Childress, unpublished data).

In the Great Lakes, white and longnose suckers both spawn in tributaries during April and May. In Wilsey Bay Creek, the number of longnose suckers was slightly less than the number of spawning white suckers, and the lack of differentiating characteristics between the species’ larvae (Snyder et al. 2004) introduced uncertainty about whether emigrating larvae were white or longnose suckers. If all larvae were longnose suckers, survivorship would still be <0.2%. In both Hibbard Creek and Lily Bay Creek, longnose far outnumbered white suckers, and the number of outmigrating larvae in Lily Bay Creek was much larger than the number of white sucker eggs deposited. Thus, it is safe to assume that these individuals were primarily longnose suckers.

The phenology of spawning was not markedly different between white and longnose suckers in our study streams, but there was large interannual variation in spawning times. Peak spawning densities were approximately one month earlier in 2012 relative to 2009 and 2013, revealing substantial flexibility in spawning phenology. The difference in timing suggests that temperature or discharge act as spawning cues rather than photoperiod. In 2013, spawning adults were present in the stream 11 days before spawning was observed, and spawning began as temperatures reached 10°C. Additionally, large quantities of eggs were deposited over a 10 day period, whereas most larvae hatched on two consecutive days. The timing of egg hatching estimated from larval otoliths is corroborated by the coincident decrease in benthic egg density. The short hatching period suggests that successfully hatched eggs were only deposited on a few days or that there is greater synchrony in egg hatching than in spawning.

Variability in sucker larval export may influence both stream and lake food-webs. Sucker eggs are large contributions of nutrients and energy to stream ecosystems (Chapter 2). Although larvae that survive and emigrate from the stream are not utilized by stream biota, less than 10% survived in the highest survival case. Still, larvae that hatch may be available to different components of the stream food web. Additionally, exported larvae become available as prey to lake predators. Suckers fall prey to a variety of fish species, including walleye and northern pike, and large influx of larvae in successful years is likely to be a boon to these predators (Beaudoin et al. 1999, Bertolo and Magnan 2005). Thus, variation in larval sucker export contributes to variation in prey availability, which could be particularly important if spring weather conditions create coherent regional patterns of larval success.

High fluctuation in fish recruitment is typical for Great Lakes fishes and for long-lived, highly fecund fishes in general (Fogarty et al. 1991, Winemiller and Rose 1993, Ludsin et al. 2014). For example, walleye exhibit highly variable larval survivorship driven by river discharge, which determines juvenile and adult year-class strength (Mion et al. 1998). Similarly, recruitment of yellow perch fluctuates due to abiotic (i.e. temperature and wind) and biotic (i.e. predation and food availability) conditions during the larval and juvenile stages (Weber et al. 2011, Kaemingk et al. 2014). The variability in survivorship during these early life stages often determines year-class strength (Houde 1989). Interestingly, adult length frequency distributions were bimodal in Wilsey Bay Creek in 2008 and 2009 for both longnose and white suckers (P. McIntyre, unpublished data). This suggests that the populations were primarily composed of a few very successful year-classes, which is consistent with our observation of enormous interannual variability in larval survivorship. Although other factors, such as predation and food availability, may also contribute to variability in year-class strength, the 20,000 fold variation in larval export is surely an important factor.

The populations we studied lie near the southern edge of the distribution of longnose suckers (Scott and Crossman 1973), which may make them vulnerable to declines or extirpation due to climate change (Parmesan 2006). Snow pack is expected to decrease in the Great Lakes region under climate change as more mid-winter melts occur and a larger proportion of the precipitation falls as rain (Cherkauer and Sinha 2010). The resulting changes in spring snow melt and flow dynamics may influence the likelihood and frequency of successful spawning events for catostomids and other spring spawning fishes. Our work underscores the importance of linking recruitment variability to particular environmental drivers so that the effects of climate change on long-term population dynamics can be predicted.

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Table 1. Reproductive success of suckers.

Stream	Year	Spawning Longnose Suckers	Spawning White Suckers	Total Eggs Deposited (10^6)	Larval Export	% Survival
Wilsey Bay Creek	2009	4,211	5,376	180	170,342	0.09
Hibbard Creek	2012	12,305	1,030	236	1,198	0.0005
Lily Bay Creek	2013	11,352	80	205	18,617,683	9.03

Figure Captions

Figure 1. Length-frequency distributions of spawning longnose suckers and the number of spawning adult suckers in the stream over the course of the sampling season.

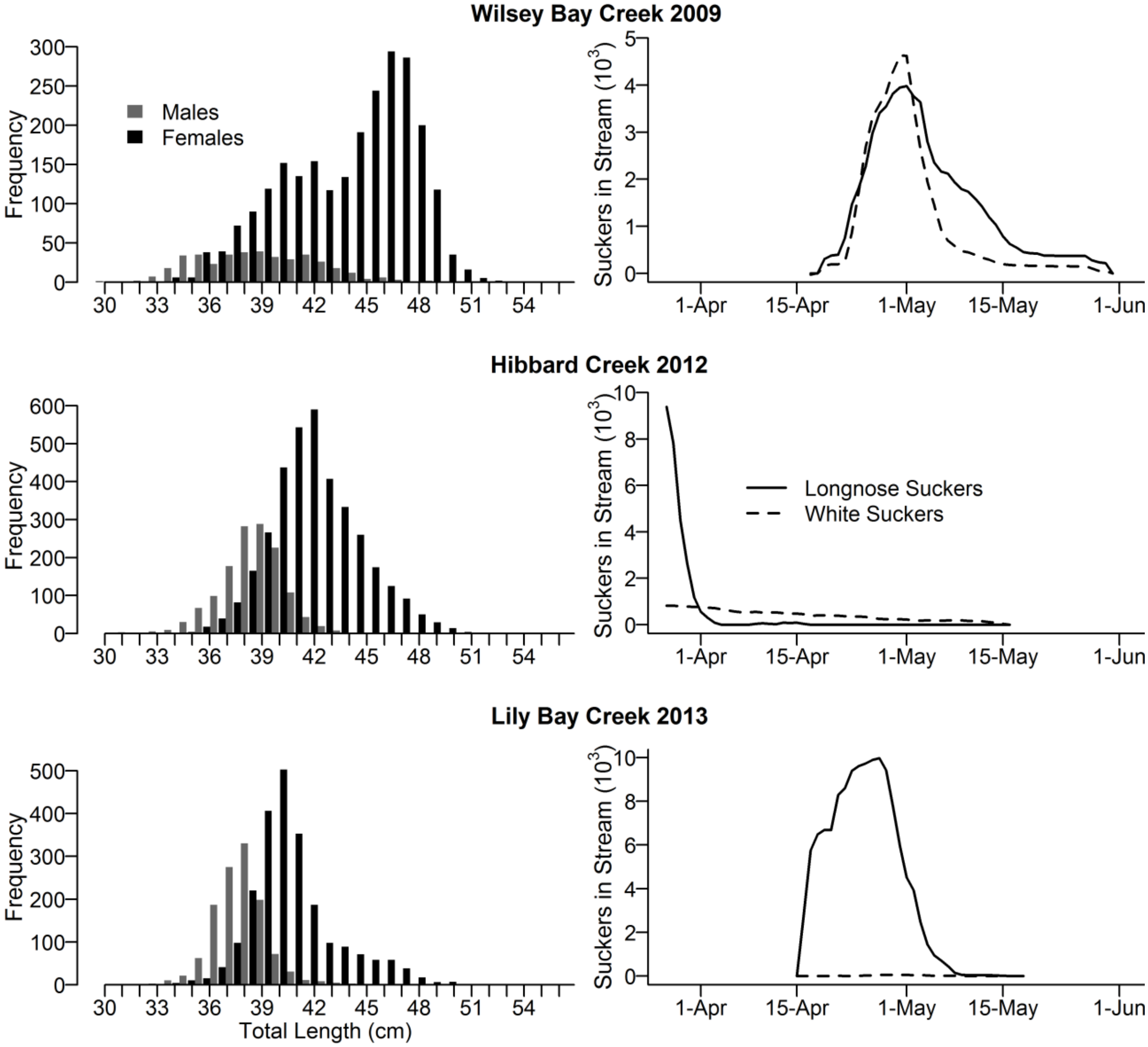
Figure 2. Mass and fecundity of longnose suckers from Lily Bay Creek and Hibbard Creek ($R^2 = 0.83$, $P < 0.001$).

Figure 3. Diel and seasonal dynamics of larval longnose sucker export. Diel figures represent larval densities in samples across a single day. Seasonal figures show daily estimates of total larval export across the drift season. Note the difference in scales for y-axes. Error bars represent ±1 standard error based on replicate samples.

Figure 4. Timing of adult migration, egg deposition, hatching, and larval export of longnose suckers in Lily Bay Creek in 2013.

Figure 5. a) Sizes of emigrating larvae in Wilsey Bay Creek in 2009. **b)** Sizes of larvae from Lily Bay Creek in 2013. Larvae were all captured during emigration except those from 11-Jul, which were captured with a dip-net. **c)** Length vs dry mass of young longnose suckers from Lily Bay Creek 2013. Darker gray indicates overlapping points.

Figure 1.



Wilsey Bay Creek 2009

Hibbard Creek 2012

Lily Bay Creek 2013

Figure 2.

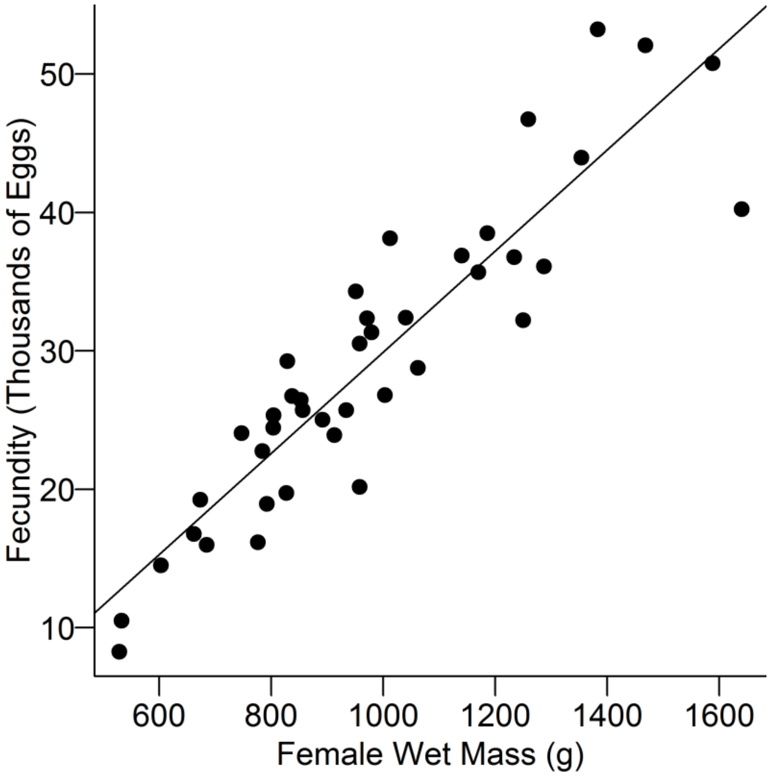

Fecundity (Thousands of Eggs)
10
20
30
40
50
600
800
1000
1200
1400
1600
Female Wet Mass (g)

Figure 3.

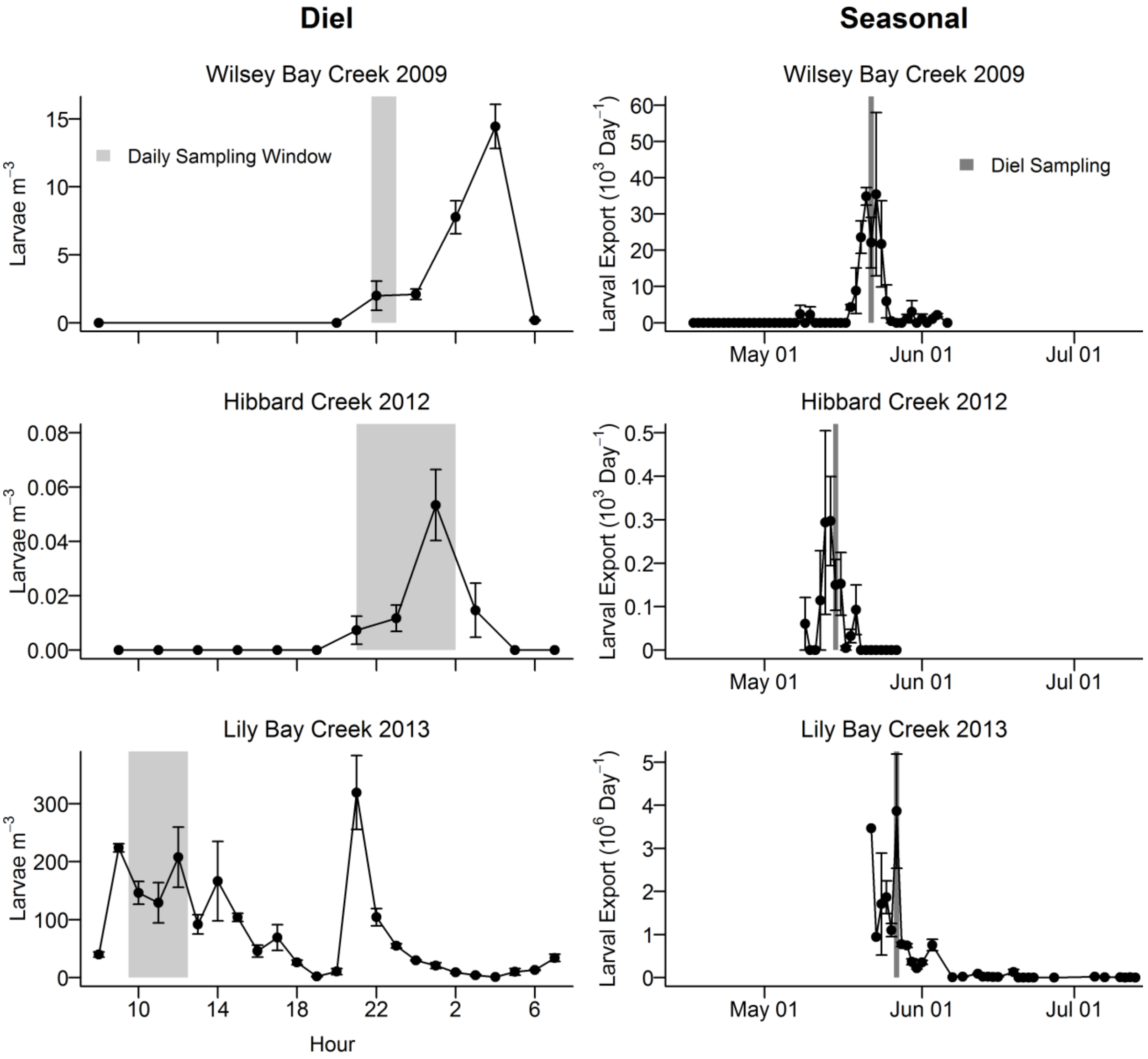

Diel
Seasonal
Wilsey Bay Creek 2009
Daily Sampling Window
Larvae m^{-3}
0
5
10
15
Wilsey Bay Creek 2009
Diel Sampling
Larval Export (10^3 Day^{-1})
0
10
20
30
40
50
60
May 01
Jun 01
Jul 01
Hibbard Creek 2012
Larvae m^{-3}
0.00
0.02
0.04
0.06
0.08
Hibbard Creek 2012
Larval Export (10^3 Day^{-1})
0
0.1
0.2
0.3
0.4
0.5
May 01
Jun 01
Jul 01
Lily Bay Creek 2013
Larvae m^{-3}
0
100
200
300
10
14
18
22
2
6
Hour
Lily Bay Creek 2013
Larval Export (10^6 Day^{-1})
0
1
2
3
4
5
May 01
Jun 01
Jul 01

Figure 4.

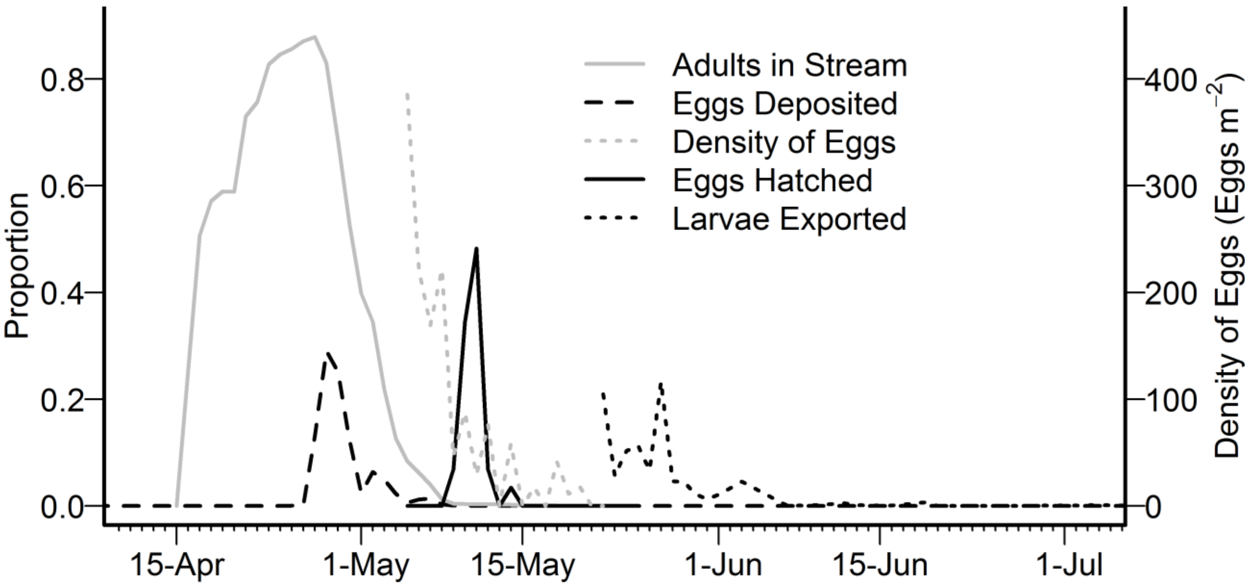
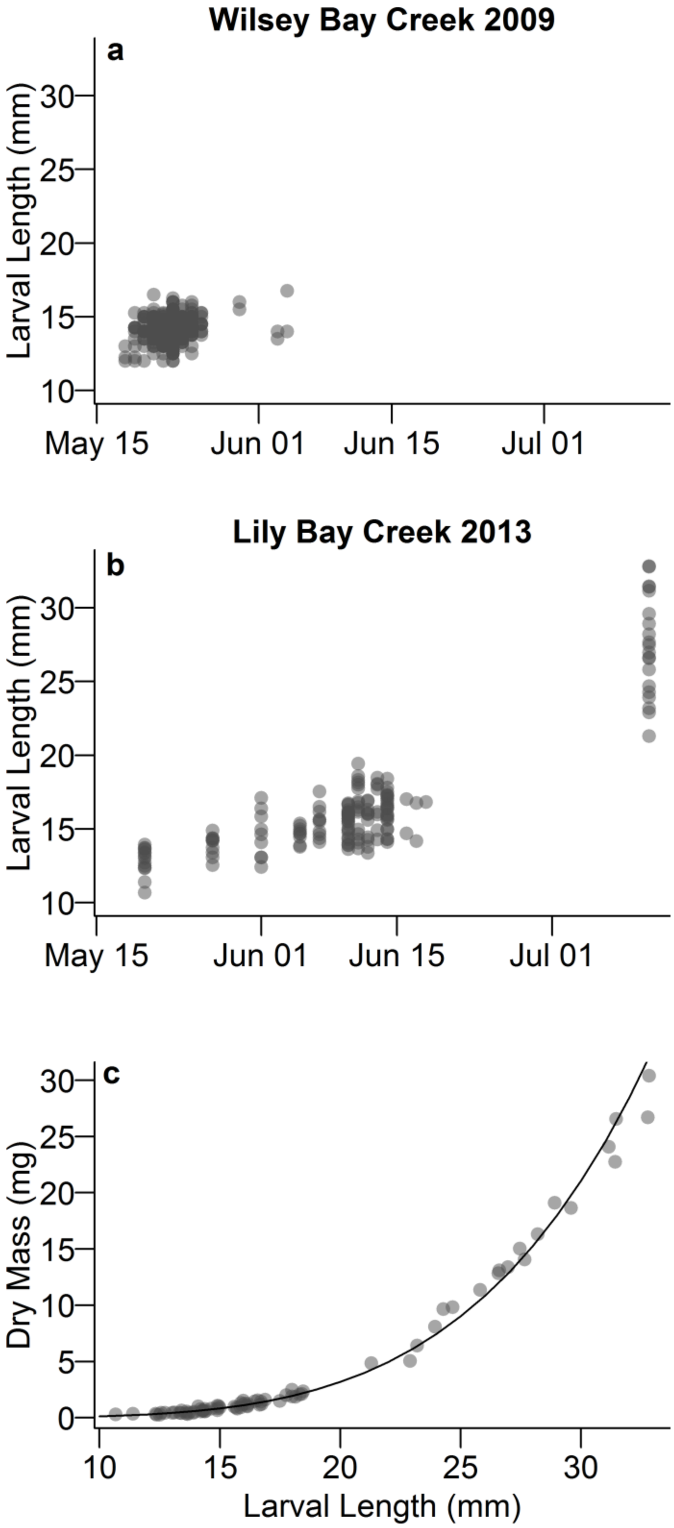

Adults in Stream
Eggs Deposited
Density of Eggs
Eggs Hatched
Larvae Exported
Proportion
0.0
0.2
0.4
0.6
0.8
Density of Eggs (Eggs m^{-2})
0
100
200
300
400
15-Apr
1-May
15-May
1-Jun
15-Jun
1-Jul

Figure 5.


Wilsey Bay Creek 2009

Lily Bay Creek 2013

Chapter 2

Multiple nutrient subsidy pathways from a migration of iteroparous fish

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Abstract

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 less than 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.

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 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, 2010). 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 10^2-10^4 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 six minutes 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; 0.7µm pore size), promptly placed on ice and analyzed for ammonium (NH_4) by fluorometry (Taylor *et al.*, 2007) within 48 hours 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 (~2° C) well below those previously observed (~7° C), and we estimate that the migration began two days before we installed the nets. Nets were emptied daily for six 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 two 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 minutes, then comparing pre- and post-incubation concentrations of dissolved N and P. Incubations were done on four days to capture a range of stream temperatures (4.9 to 12.5º 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 minute 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 hours). Homogenized subsamples from nine ovaries were analyzed for N content using an elemental analyzer (GasBench II, Thermo Scientific^{TM}) 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 outmigration, 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 A).

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 mineralized 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, homogenized, 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-6 May 2013. After collection, glass discs were kept frozen in darkness until extraction of chlorophyll *a* in a 90% buffered ethanol (24h, 20°C). Extracts were analyzed 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 3,505 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 ($^{\circ}$C) and fish length (cm) for both NH_4 ($r^2 = 0.65$, $P < 0.001$, $\log_{10}[NH_4\ \mathrm{Excretion}] = 1.37*\log_{10}[\mathrm{Temp}]+1.5*\log_{10}[\mathrm{Length}]-1.88$) and SRP ($r^2 = 0.42$, $P < 0.001$, $\log_{10}[\mathrm{SRP\ Excretion}] = 0.16*\log_{10}[\mathrm{Temp}]+2.23*\log_{10}[\mathrm{Length}]-2.73$). 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 A, Fig. A1). Females contained an average of 171 g (wet mass) of eggs and collectively deposited an estimated 1,161 ± 9 kg (wet mass) of eggs. Egg dry mass was 36.3 ± 0.3% (mean ± SE) of egg wet mass; 10.7 ± 0.1% of egg dry mass was N and 1.1 ± 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 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 $\mu g\ L^{-1}$ vs. 391 $\mu g\ L^{-1}$ 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 less than 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) was composed of 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 4,524 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 equaled daily export of NH_4 and SRP during the migration. The timing of estimated mineralization 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 deliver important nutrient subsidies to spawning grounds. Rather, decay of gametes and recycling of wastes by live fish are sufficient to generate ecologically 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 generalize 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 (Vanni, 2002; Schindler, Knapp & Leavitt, 2001; 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 hours (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 recognized 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, 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 two-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 th 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 and 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 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 and Whiles, 2006), and aquatic insects become an important food source for riparian insectivores as they emerge to reproduce (Nakano and 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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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 totaled <2% of NO_3 export during the study.

Fig. 2. Nutrient dynamics during egg decomposition in microcosms. Error bars represent ±1 SE.

Fig. 3. (a,b) Instream nutrient dynamics and modeled 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.

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.

Figure 1.

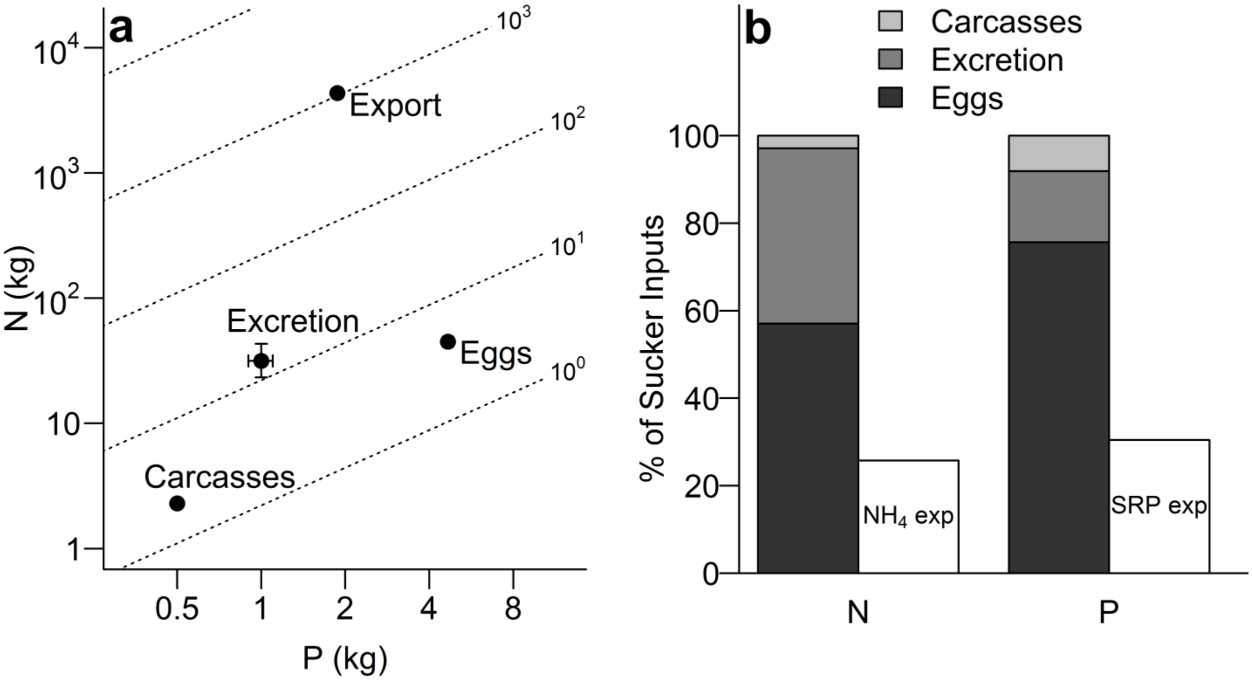

a
10^4
10^3
10^2
10
1
N (kg)
0.5
1
2
4
8
P (kg)
10^3
10^2
10^1
10^0
Export
Excretion
Eggs
Carcasses
b
Carcasses
Excretion
Eggs
100
80
60
40
20
0
% of Sucker Inputs
NH_4 exp
SRP exp
N
P

Figure 2.

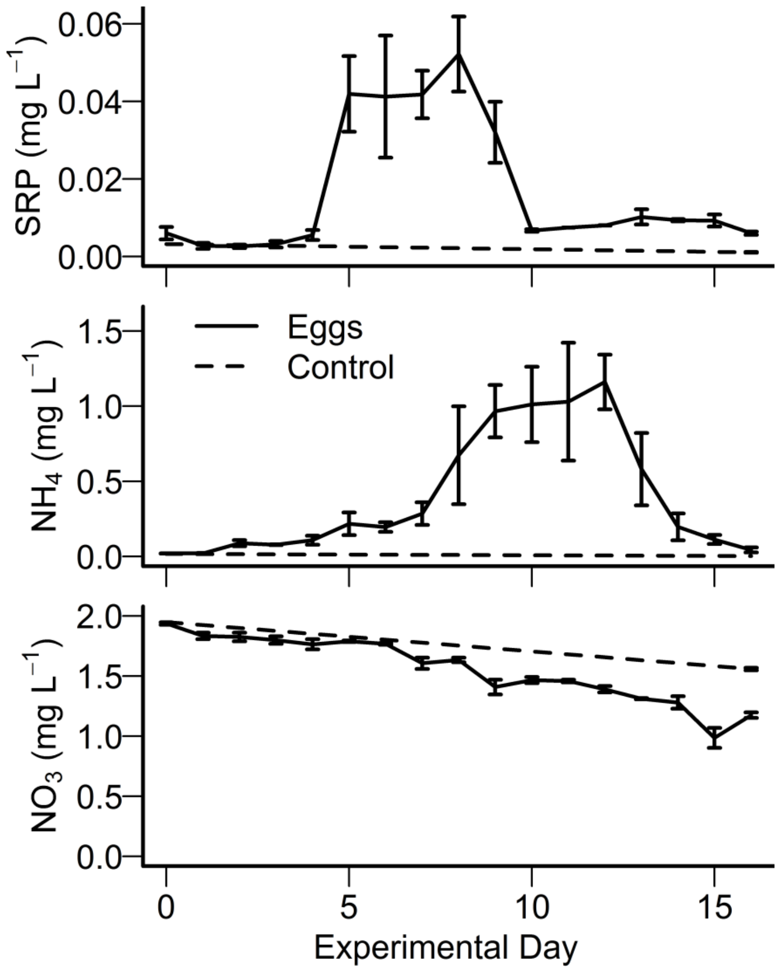

SRP (mg L^{-1})
0.06
0.04
0.02
0.00
NH$_4$ (mg L^{-1})
1.5
1.0
0.5
0.0
Eggs
Control
NO$_3$ (mg L^{-1})
2.0
1.5
1.0
0.5
0.0
0
5
10
15
Experimental Day

Figure 3.

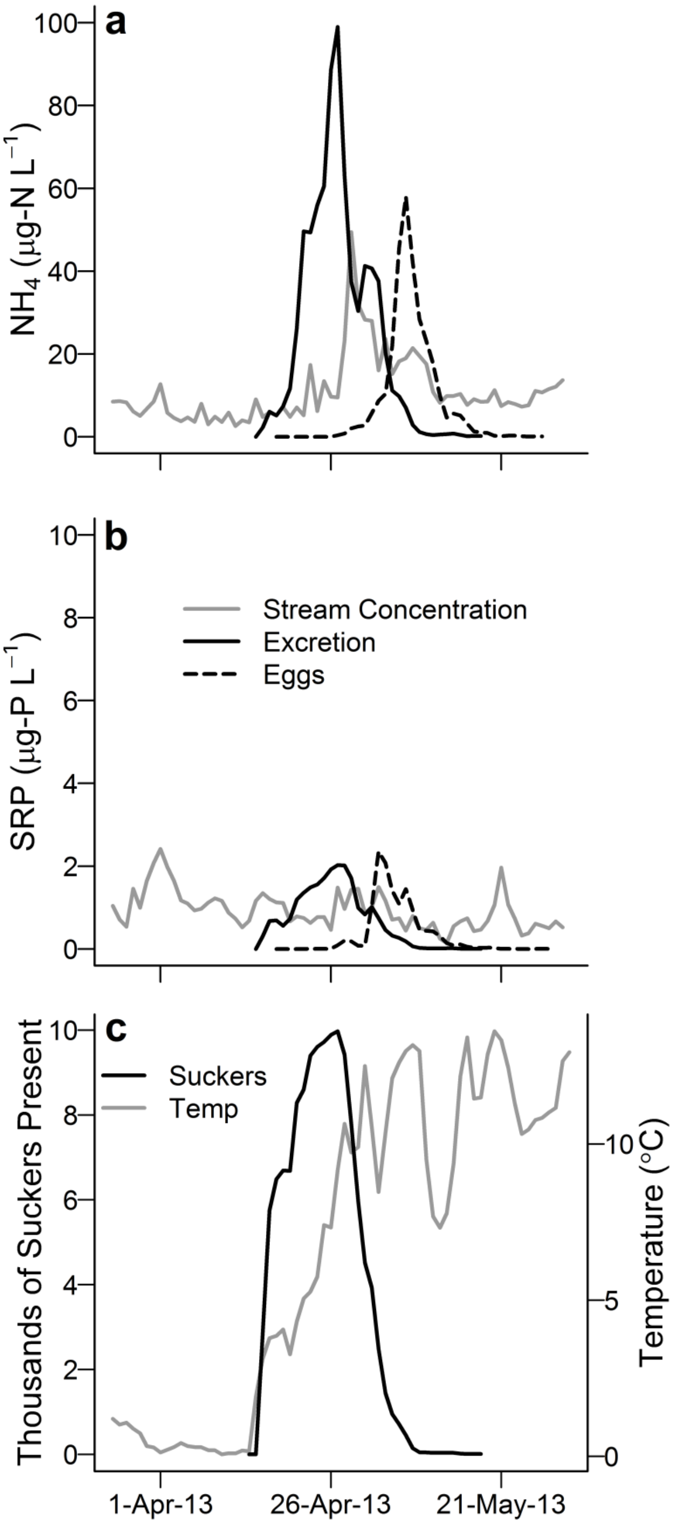
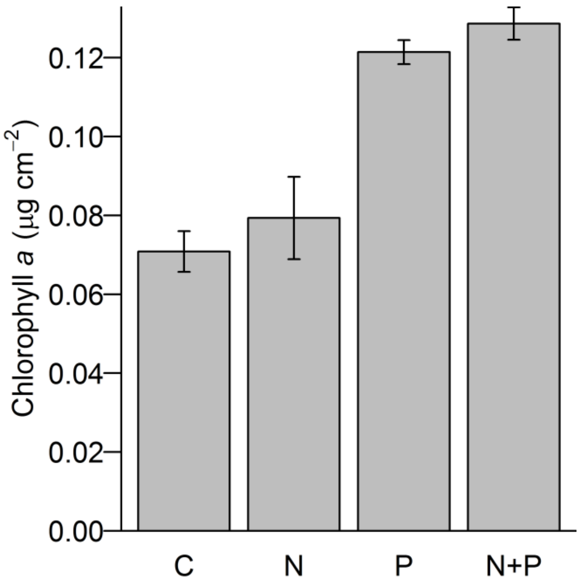

a
NH$_4$ (μg-N L^{-1})
100
80
60
40
20
0
b
SRP (μg-P L^{-1})
10
8
6
4
2
0
Stream Concentration
Excretion
Eggs
c
Thousands of Suckers Present
10
8
6
4
2
0
Suckers
Temp
Temperature (°C)
10
5
0
1-Apr-13
26-Apr-13
21-May-13

Figure 4.



Appendix 2.1

Estimation of nutrient inputs from sucker eggs

To estimate the nutrient contribution from sucker eggs during the spawning migration, we combined ovary mass estimates with measured nutrient and dry matter contents of eggs. To estimate ovary mass, we collected data on ovary mass and total length of adult females captured as they entered our focal streams to spawn. Reproductive investment generally scales as a power function of body size, and that was the case for longnose suckers (Fig. A1). We used linear regression to fit $\log_e$-transformed total length (TL) and $\log_e$-transformed ovary wet mass (OM) ($R^2 = 0.80$, $P < 0.001$; $OM = 0.00005703 * TL^{3.929}$). To extrapolate individual estimates of ovary mass to the population level, the length distribution of females (n = 2141, Fig. A2) was sampled with replacement to obtain lengths for unmeasured individuals (n = 5000). Ovary wet mass was predicted for each individual in the modeled population using the regression equation, and we converted egg mass into nutrient units by multiplying by dry matter and N or P contents of eggs. Nutrient contribution and egg mass were estimated at the individual level and summed to develop an estimate for the whole population. To develop bootstrapped confidence intervals for the nutrient input estimates, we resampled distributions of dry matter and nutrient contents 10,000 times and carried through the prediction error associated with the regression between size and ovary mass.

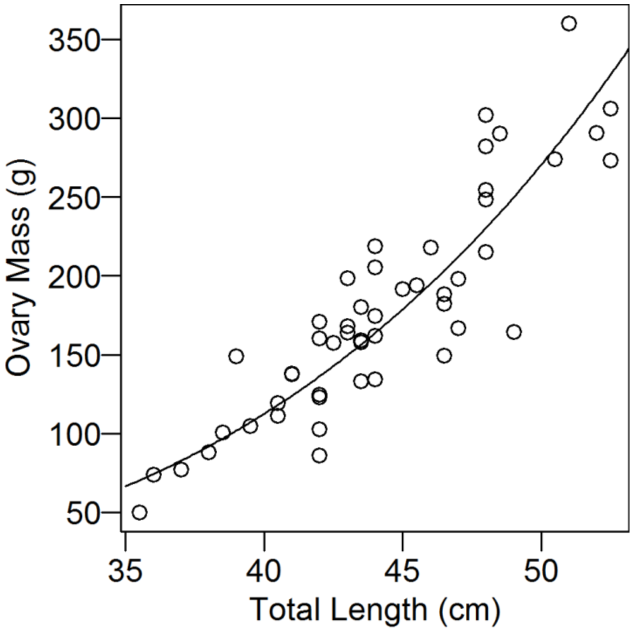


Figure A1. Relationship between total length and ovary mass among female longnose suckers.

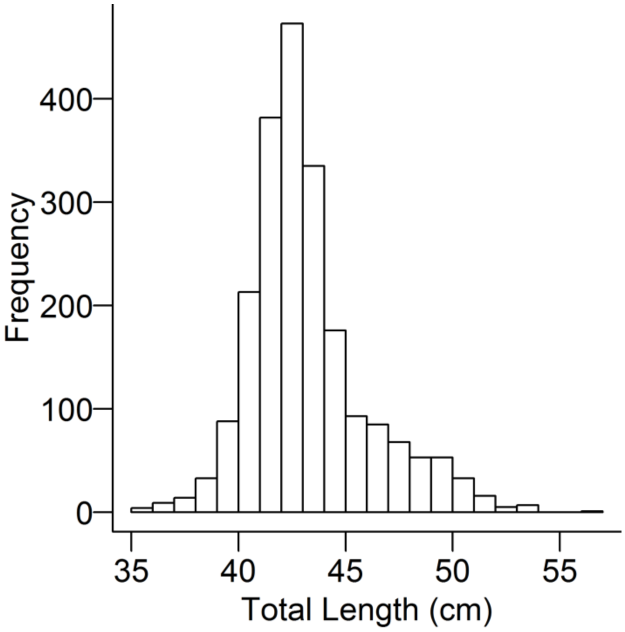


Figure A2. Frequency histogram of total length for female longnose suckers captured in Lily Bay Creek during the spawning migration in 2013.

Chapter 3

Spawning behavior during fish migrations modulates ecosystem-level effects of nutrient subsidies

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Prepared for submission to *Ecology* with co-author Peter B. McIntyre

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Abstract

Migratory animals can have profound impacts on ecosystem functioning. In streams, salmon are well known for their contrasting influences on primary productivity through nutrient delivery, which enhances production, and disturbance during nest building, which reduces algal biomass and primary production. However, many migratory fish do not disturb the substrate significantly, and this aspect of spawning behavior may alter the ecological response to fish migrations. To determine the influence of nutrient subsidies from fish migrations in the absence of major disturbance, we compared nutrient dynamics and limitation and stream metabolism during spawning migrations of suckers (*Catostomus* spp.) in Lake Michigan tributaries with and without migration barriers. Although suckers deliver both nitrogen and phosphorus, NH_4-N concentrations were elevated during the sucker migration relative to reference sites across a wide range of sucker abundance, whereas phosphate concentrations did not respond significantly to the presence of suckers. Because nutrient diffusing substrates demonstrated P limitation at all sites and additional N limitation at two-thirds of sites, high demand for P relative to supply likely contributed to the observed nutrient responses. Gross primary production (GPP) and ecosystem respiration (ER) responded to large changes in temperature, discharge, and light in the period from snow melt to summer. After accounting for seasonal dynamics, GPP was enhanced in the presence of suckers, but ER showed no response. This result contrasts with previous work documenting strong ER responses to salmon, which disturb the substrate during spawning and subsequently die in the stream. Because suckers do not dig in the substrate, they fertilize streams without attendant disturbance effects. Our results highlight that spawning behavior can alter the direction of ecosystem responses to fish migrations.

Introduction

Animal migrations link disparate ecosystems by transferring materials and creating new food web interactions, resulting in large and lasting impacts on ecosystem dynamics and productivity (Bauer and Hoye 2014). The role that particular species play in material transport depends on behavioral and life history traits (Marczak et al. 2007, Flecker et al. 2010). As migrations are threatened across the globe (Humphries and Winemiller 2009), it is critical to determine which species influence ecological processes and how life history and behavioral characteristics regulate their influence.

Migratory fish can deposit nutrients and energy as carcasses, gametes, and waste products to their spawning grounds (Varpe et al. 2005, Janetski et al. 2009), but life history mediates the type of materials delivered. Species that die en masse after spawning (i.e., semelparous fishes) deliver many carcasses, whereas species that spawn multiple times (iteroparous fishes) do not. Additionally, some migratory species disturb large areas of the stream bed to build nests during spawning with major impacts on stream biota and processes (Moore and Schindler 2008, 2010), while others broadcast their gametes widely with minimal disturbance to the substrate. Together these behavioral and life history characteristics have the potential to alter the ecosystem role of fish migrations. Most research on the impacts of fish migrations has focused on Pacific salmon, which die after spawning once and disturb large areas of the streambed. Understanding the influence of species with other life history and behavioral characteristics is critical for determining the ecological role of fish migrations more generally.

Salmon deliver nutrients from the ocean to their freshwater spawning grounds (Naiman et al. 2002, Janetski et al. 2009). However, their strongest effect is often disturbance during nest building (Moore et al. 2004) through which they consistently increase ecosystem respiration (ER) (Holtgrieve and Schindler 2011, Levi et al. 2013). In contrast, responses of gross primary production (GPP) to salmon migrations can be positive or negative and may depend on substrate size (Holtgrieve and Schindler 2011, Levi et al. 2013), which mediates the magnitude of disturbance during nest building (Freeman et al. 2003).

Knowledge of how salmon influence ecological processes is unlikely to translate to other species because of life history and behavioral differences, which raises the question: how do these species influence ecosystem processes? Suckers (Catostomidae) provide an opportunity to test the generality of salmon findings to iteroparous species and species that do not represent a major disturbance. Suckers migrate to spawn annually in many streams across North America and often reach high densities during spawning periods. In Great Lakes tributaries, migrations range in size from hundreds to thousands of fish in small streams up to a million in large rivers (Klingler et al. 2003, Burtner et al. 2011, Childress et al. 2014). These migrations can deliver nutrients that enhance concentrations many times over background levels (Childress and McIntyre *in press*), leading to increased algal and invertebrate growth (Childress et al. 2014). The increase in algal production contrasts with scouring of algae during salmon migrations

(Moore et al. 2004), and suggests that ecosystem function might respond differently to migrations of different species.

Beyond their contrasting geographic and life history patterns, salmon disturb the substrate during spawning but suckers do not, which may also mediate the response in ecosystem function. In contrast to salmon, which can reduce algal biomass (Moore and Schindler 2008) and GPP but increase ER through bioturbation (Holtgrieve and Schindler 2011, Levi et al. 2013), suckers are broadcast spawners, depositing adhesive eggs that settle into crevices and depressions and so do not cause much disturbance during spawning activity (Walton 1980, Page and Johnston 1990). Because suckers do not disturb large swaths of the streambed but still deliver nutrients, suckers may have a smaller influence on ER but enhance GPP through fertilization. To evaluate this prediction and the role of spawning behavior in ecosystem responses to fish migrations, we examined dynamics of ecosystem metabolism and nutrients in streams with and without barriers to spawning migrations of iteroparous longnose suckers (*Catostomus catostomus*).

Methods

We measured nutrient concentrations, nutrient limitation, and ecosystem metabolism in Lake Michigan tributaries in Door County, WI. The study area is a mix of agriculture, coniferous forest, and hardwood forest. The sites were all in low-gradient, second-order streams, featuring sand- and silt-dominated pools alternating with short cobble-bottomed riffles (see Appendix A).

To determine the timing and size of the sucker migration, we installed trap nets in two streams, Lily Bay Creek and Hibbard Creek, in 2012 and 2013. In 2012, we deployed a single net facing upstream that spanned 80% of the stream, providing robust data for the timing of the migration but not the magnitude. Nets were checked daily and all fish were sexed, counted, and released to continue their migration. All incoming migrants were marked with a dorsal fin clip to enable identification of recaptures. In 2013, two trap nets spanning the entire stream were installed, providing robust data on the timing and magnitude of the migration. One net faced downstream and caught incoming migrants, while the other faced upstream and caught out-migrating fish. Our observations indicated that the first fish migrated roughly two days before nets were installed, and all out-migrating fish without a fin clip were assumed to have entered in equal numbers on those two days.

Nutrient Dynamics

Nutrient dynamics were assessed in the spring of 2012 and 2013 at 10 sites across 8 streams. Three sites were located above fish barriers (impassable road culverts) to serve as reference sites, and seven sites received migrations of longnose suckers (*Catostomus catostomus*) and white suckers (*Catostomus commersonii*) ranging from <500 to >10,000 individuals. To determine nutrient dynamics, we sampled stream water every other day for 62 days in 2012 and 66 days in 2013. Samples were filtered (Whatman GF/F 0.7 µm) in the field and analyzed for ammonium (NH_4-N) within 48 hrs of collection using fluorometry (Holmes et al. 1999, Taylor et al. 2007) or frozen for subsequent analysis of nitrate (NO_3-N) and soluble reactive phosphorus (SRP) by standard colorimetric methods (APHA 1998). Nutrient data were only available for seven streams in 2013.

The response of NH_4-N and SRP to the presence of suckers was evaluated using linear mixed effects (LME) models. Data on sucker migration phenology was available for two of the sucker streams as described above. Daily visual observations indicated that migration timing was similar across sites. To test for a sucker effect on NH_4-N and SRP, we considered suckers to be present throughout the period when >5% of the migrating population was present in both of the streams with detailed abundance measurements. The LME models included sucker presence, treatment (reference or sucker migration), and their interaction as predictors and accounted for non-independence of measurements from the same stream or year (each represented by fitting a random intercept term). A significant interaction between sucker presence and treatment was interpreted as indication of divergence between sucker and reference streams when suckers were present. Nutrient data were natural log-transformed to meet the assumption of normality.

Nutrient Limitation

To evaluate nutrient limitation of periphyton, nutrient diffusing substrata (NDS) (Tank et al. 2007) were deployed in all 8 study streams from April 16th to May 6th 2013, which coincided with the sucker run. In streams with migration barriers, experiments were conducted downstream where suckers were present. Plastic containers were filled with agar amended with nitrogen (0.5M NH_4Cl), phosphorus (0.5M KH_2PO_4), nitrogen and phosphorus (0.5 M NH_4Cl + 0.5 M KH_2PO_4), or no nutrients (n = 6 per treatment), and a fritted glass disc separated the agar from the water column. After collection, glass discs were kept frozen in darkness until extraction of chlorophyll *a* in 90% pH-buffered ethanol (24h, 20°C). Extracts were analyzed by fluorometry, including an acidification step. NDSs washed out in two streams, so no results are available for these sites. The effect of nutrient amendments on chlorophyll *a* accrual was evaluated using two-way factorial ANOVAs of the effects of N and P. We interpreted significant main effects as evidence of primary limitation and a significant N-P interaction in the presence of a single primary effect as evidence of secondary limitation (Tank and Dodds 2003).

Whole-Stream Metabolism

We estimated whole-stream metabolism in a subset of four streams in the spring of 2013. Lily Bay Creek (44.8471 N, 87.2672 W) and Hibbard Creek (44.9865 N, 87.1748 W) received spawning migrations of around 10,000 longnose suckers (*Catostomus catostomus*) and white suckers (*Catostomus commersonii*). Fish Creek (45.1281 N, 87.2401 W) and Fisher Creek (44.8647 N, 87.2276 W) had fish barriers <300 m from their mouths and served as reference sites to document spring dynamics of metabolism in the absence of suckers.

Water level was logged every six minutes in each stream using a HOBO® U20 (onsetcomp.com) and converted to discharge using a power-function relationship across a range of water levels (all $R^2 > 0.97$; Appendix A). Discharge measurements at the logger and ~400m upstream at two of the study reaches indicated loss of ~3% of the water within the reaches. Light was measured at the stream benthos of each site as lux using a HOBO® UA-002 Pendant.

We estimated stream metabolism using a single-station open-channel method (Odum 1956) from diel fluctuations in dissolved oxygen (DO) concentration. Sites were selected to maximize homogeneity within the reach. Dissolved oxygen and temperature were recorded at 10 minute intervals using HOBO® U26 (onsetcomp.com) loggers. Changes in stream DO concentration result from the production of oxygen through gross primary production (GPP), consumption through ecosystem respiration (ER), and exchange with the atmosphere. To estimate atmospheric exchange, the reaeration coefficient (K) was estimated using a published relationship between velocity, depth, discharge, and K (Raymond et al. 2012, Equation 7) using daily averages for stream characteristics. Gas exchange was then adjusted for stream temperature using Schmidt numbers (Wanninkhof 1992) and multiplied by mean depth to obtain gas transfer velocity. After accounting for gas exchange, respiration was estimated by extrapolating the rate of change of DO during the night, when no primary production occurs, to apply to the whole day. GPP was then estimated as the difference between net oxygen change and ER after accounting for atmospheric exchange. Metabolism was also estimated using a Bayesian metabolism model that simultaneously fits parameters for gas exchange, primary production, and respiration (Holtgrieve et al. 2010), which yielded qualitatively similar results. Bayesian models did not converge on parameter values on dates with low variability in oxygen concentrations; therefore, we present only the results from the Odum (1956) method.

To determine the influence of seasonal dynamics and the fish migration on stream metabolism, we fit separate time series models to GPP and ER in each stream. We constructed a model to account for known drivers of stream metabolism and temporal autocorrelation and included sucker abundance as a continuous variable to test for a sucker effect. In contrast to the nutrient analysis, we used sucker abundance because stream-specific measurements were available for both sucker sites. Based on previous studies on stream metabolism, we included temperature, discharge, and their interaction as covariates in all models, and light was included in GPP models (Mulholland et al. 2001, Roberts et al. 2011, Demars et al. 2011). Suckers were included as a predictor in the reference stream models to test for a spurious effect of suckers due to correlation with some unmeasured seasonal variation not included in the model; average abundance for the two sucker streams was used in reference stream models. This ecologically-based modeling approach could result in over-fitting models; however, more parsimonious models yielded similar results for sucker parameters in every case. Outliers were incorporated into the time series model for GPP on two dates in Lily Bay Creek, the most productive stream, to account for aberrant values. Other model residuals did not show evidence of outliers.

Results

Nutrient Dynamics

The presence of suckers was associated with a 44% increase in NH_4-N concentrations, while reference sites remained at baseline concentrations throughout the season (Fig. 1). Sucker streams had a median NH_4-N concentration of 18 μg-N L^{-1} during the migration, while reference sites had a median of 11 μg-N L^{-1}. The LME model for NH_4-N showed that the presence of suckers increased NH_4-N significantly ($t = 3.07$, $P = 0.002$, see Appendix B for full model output). Elevated NH_4-N concentrations during the first two weeks of sampling in 2013 were observed in all five streams with a lake upstream; their high NH_4-N during snow melt fell rapidly as temperatures warmed. In contrast to NH_4-N, there was no apparent increase in SRP concentrations during the sucker migration (LME, interaction of sucker presence and treatment: $t = -0.625$, Appendix B). NO_3-N levels closely tracked discharge during the spring melt with no evidence of sucker influence, and background concentrations ranged from 50-2000μg-N L^{-1} (results not shown).

Nutrient Limitation

Nutrient diffusing substrate experiments demonstrated a positive algal response to P additions across all streams (Fig. 2, see Appendix C for full ANOVA results). Additionally, N enhanced algal accrual in three streams, and a fourth stream exhibited an N response only in the presence of added P.

Stream Metabolism

Both GPP and ER exhibited large seasonal variability in all four study streams. GPP and ER were elevated during the sucker migration (Fig. 3); however, these metabolic changes also coincided with changes in abiotic conditions (Fig. 4). In the time-series models of GPP, temperature, discharge, and light were all important predictors of within site variation (Table 1). Suckers were a significant predictor in the sucker streams, and there was no evidence of a spurious sucker effect in reference streams. At the site level, lower GPP was associated with riparian shading, but shading did not prevent a clear response to the sucker in Hibbard Creek. In contrast, ER did not respond to the sucker migration (Table 1), and variability in ER within sites over the course of the season was largely explained by changes in temperature and discharge.

Discussion

Our results demonstrate that suckers can elevate nutrient concentrations leading to increased GPP during spawning. This finding lengthens the causal chain of ecosystem changes attributable to migratory fish that do not die en masse. Importantly, our results contrast with evidence that salmon increase ER but often dampen GPP during spawning (Holtgrieve and Schindler 2011, Levi et al. 2013), suggesting that spawning behavior mediates ecosystem effects of fish migrations.

Experimental nutrient additions enhanced algal accrual at all sites, indicating that nutrient inputs from migrating suckers have the potential to increase algal growth through provisioning of limiting nutrients (see also Childress et al. 2014). Suckers deliver large quantities of both N and P to their spawning grounds in the form of excretion and eggs; our previous work showed that suckers deposited >300% more P than was exported as SRP in the spring of 2013 in Lily Bay Creek (Childress and McIntyre *in press*). Although the primary land cover in the study area is agriculture and background inorganic N concentrations were as high as 2 mg L^{-1}, fish still had a measureable effect on NH_4-N. The significant elevation of NH_4-N but not SRP during the migration suggests a higher demand:supply ratio for P than for N. Enhanced nutrient concentrations at the stream mouth represent excess or regenerated nutrients, thus P uptake apparently masked the presence of fish-derived P inputs.

The delivery of growth-limiting nutrients appears to be responsible for the observed increase in GPP during the 32 day sucker migration, but GPP and ER also showed strong responses to the large changes in abiotic conditions during the spring. Spring is a highly productive and dynamic season in temperate streams because temperatures are rising and leaf cover does not yet shade the stream (Roberts et al. 2011). Spring fish migrations, which include Atlantic salmon, many clupeids, as well as suckers, coincide with these conditions, enhancing nutrient availability for primary production at a time when algae may be readily able to respond. In spite of background variability associated with seasonal changes in light, temperature, and discharge, GPP showed a significant response to sucker abundance.

In contrast to the increased GPP and unchanged ER that we observed during sucker migrations, salmon strongly increase ER and have variable effects on GPP governed by the strength of the disturbance (Holtgrieve and Schindler 2011, Levi et al. 2013). These contrasting results are likely driven by differences in spawning behavior. Salmon create a major disturbance to their spawning streams as they excavate nests. In contrast, suckers are generally broadcast spawners (Page and Johnston 1990) that do not disturb substrates during spawning. This interpretation is supported by the finding that salmon can increase GPP when disturbance effects are lower because of larger substrate size (Levi et al. 2013). Thus, although suckers and salmon both deliver nutrients, it appears that fertilization is the dominant effect of sucker migrations, while disturbance during salmon migrations typically elevates ER and dampens GPP (Holtgrieve and Schindler 2011).

The response of ecosystem processes to fish migrations in general appears to be modulated by both the magnitude of nutrient contributions relative to background availability and the strength of disturbance associated with spawning behavior (Fig. 5). Life history attributes such as parity, body size, reproductive investment, timing of transitions among life stages, and early life mortality will influence the magnitude of added nutrients from species and the response of GPP. For example, iteroparous species will have smaller per capita material contributions at the annual scale than semelparous species, but contributions from eggs and gametes are still sufficient to enhance productivity (Childress and McIntyre *in press*, Durbin et al. 1979, Walters et al. 2009). Some life histories minimize the influence of fish migrations on ecosystem processes. For example, amphidromous gobies live in streams as adults but have an oceanic larval stage, returning to freshwaters at a small size. Because they both spawn and achieve most of their growth in the same habitat, they are unlikely to transfer large quantities of nutrients during their migrations. Although these variations in nutrient delivery could also influence ER if heterotrophic activity is nutrient limited (Mulholland et al. 2001); our result that suckers did not enhance ER suggests that nutrient delivery alone in the absence of bioturbation is not sufficient to increase ER.

Bioturbation during spawning increases ER but decreases GPP, and variation in disturbance caused by different species mediates the ecosystem response to their migrations (Fig. 5). In addition to the increasingly recognized importance of disturbance during salmon migrations (Moore and Schindler 2008), other nest-building species, such as sea lamprey, also have lasting effects on resident biota through disturbance (Hogg et al. 2014). In contrast, the broadcast spawning behavior of catostomids and clupeids leads to fertilization without significant disturbance, yielding enhanced GPP but no effect on ER. Thus, disturbance is the primary influence on ER, while GPP responses are determined by the interaction of nutrient addition and disturbance.

Ultimately, these species characteristics will interact with migration size and environmental context to determine the influence of migrations. For example, light availability appeared to influence the magnitude of the GPP response to the sucker migration in this study although the small sample size inhibits a direct test of the role of light. Additionally, the susceptibility of ecosystems to fish disturbance (Rüegg et al. 2012) and the background nutrient availability (Marczak et al. 2007, Flecker et al. 2010) also influence the ecological response. Although many of our study watersheds contained over 50% agriculture, it appears that nutrients generally limit algal production in the study region; hence the addition of nutrients during the fish migration influenced productivity. Our sites receive moderate anthropogenic nutrient inputs, and more oligotrophic streams are likely to respond more dramatically while streams with heavily agricultural watersheds may not respond to sucker migrations.

Our understanding of the ecosystem role of fish migrations will benefit from studies on species with other combinations of life history and behavioral attributes. Suckers provide an informative contrast to salmon because they differ in both disturbance and life history. Our results provide a basis for predictions of the effects of other species based on their characteristics. For example, steelhead are iteroparous but disturb the substrate, thus their influence may be biased more towards depression of GPP than salmon because of smaller nutrient contributions. Because fish migrations can have large and variable influence on ecosystem processes, exploring the role of species characteristics in modulating this influence is necessary to hone our understanding of their ecological role.

Acknowledgements

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Table 1. Coefficients for time series models testing the effect of suckers on stream metabolism while accounting for abiotic conditions. Italicized streams received a sucker migration. Positive coefficients indicate a positive relationship between GPP or ER and the predictor. Standard errors are in parentheses and bold indicates coefficients that are significantly different than zero (95% CI).

Site	**ar1**	**Temp**	**Q**	**Temp:Q**	**Suckers**	**Light**
			Gross Primary Production			
Lily Bay Creek	**0.37 (0.14)**	**0.81 (0.08)**	**1.13 (0.1)**	**0.41 (0.08)**	**0.37 (0.08)**	**0.18 (0.04)**
Hibbard Creek	0.16 (0.16)	0.1 (0.09)	0.02 (0.12)	-0.01 (0.07)	**0.19 (0.08)**	**-0.06 (0.03)**
Fish Creek	**0.48 (0.12)**	**0.43 (0.07)**	**0.64 (0.1)**	**0.44 (0.08)**	0.07 (0.07)	**0.1 (0.04)**
Fisher Creek	0.07 (0.14)	**0.4 (0.08)**	0.13 (0.1)	**-0.28 (0.07)**	-0.05 (0.05)	0.06 (0.04)
			Ecosystem Respiration			
Lily Bay Creek	**0.97 (0.03)**	**2.3 (0.24)**	**1.17 (0.23)**	**0.7 (0.19)**	-0.06 (0.29)	N/A
Hibbard Creek	0.32 (0.22)	**0.64 (0.18)**	**0.89 (0.24)**	0.09 (0.16)	0.15 (0.17)	N/A
Fish Creek	**0.41 (0.13)**	-0.03 (0.12)	**0.98 (0.13)**	**2.5 (0.37)**	0.03 (0.08)	N/A
Fisher Creek	0.14 (0.14)	**0.54 (0.1)**	**0.37 (0.13)**	-0.16 (0.08)	-0.02 (0.07)	N/A

Figure Captions

Figure 1. Mean nutrient concentrations for streams with a sucker migration (suckers, $n = 7$) and those without (reference, $n = 3$) over the course of the migration. NH_4-N became significantly elevated during the migration, while there was no significant effect on SRP. Error bars represent ±1 standard error.

Figure 2. Chlorophyll *a* growth on nutrient diffusing substrata amended with no nutrients (C), nitrogen (N), phosphorus (P), or both N and P (NP). Stars indicate significant effects of N, P, or their interaction ($* = P < 0.05$, $** = P < 0.01$), and letters above bars indicate nutrient limitation. Error bars represent ±1 standard error.

Figure 3. Spring dynamics of stream metabolism in reference (black/gray lines) and sucker (colored lines) sites. Blue represents the absence of suckers, and increasingly yellow colors indicate high abundance.

Figure 4. An example of stream metabolism dynamics relative to abiotic changes in a reference stream (Fish Creek). Stream metabolism exhibited responses to shifting abiotic conditions in all study streams.

Figure 5. Conceptual figure depicting how variability in substrate disturbance and nutrient delivery alter the per capita influence of fish migrations on gross primary production and ecosystem respiration with examples of the role of particular species groups. Nutrient contributions depend on mortality rate, body size, fecundity, and excretion rates. Disturbance of the substrate is determined by the extent to which spawning is associate with bioturbation for nest building. Gobies refer to amphidromous gobies, which have an oceanic larval phase, but because they both grow and spawn in freshwaters, they do not contribute substantial nutrients.

Figure 1.

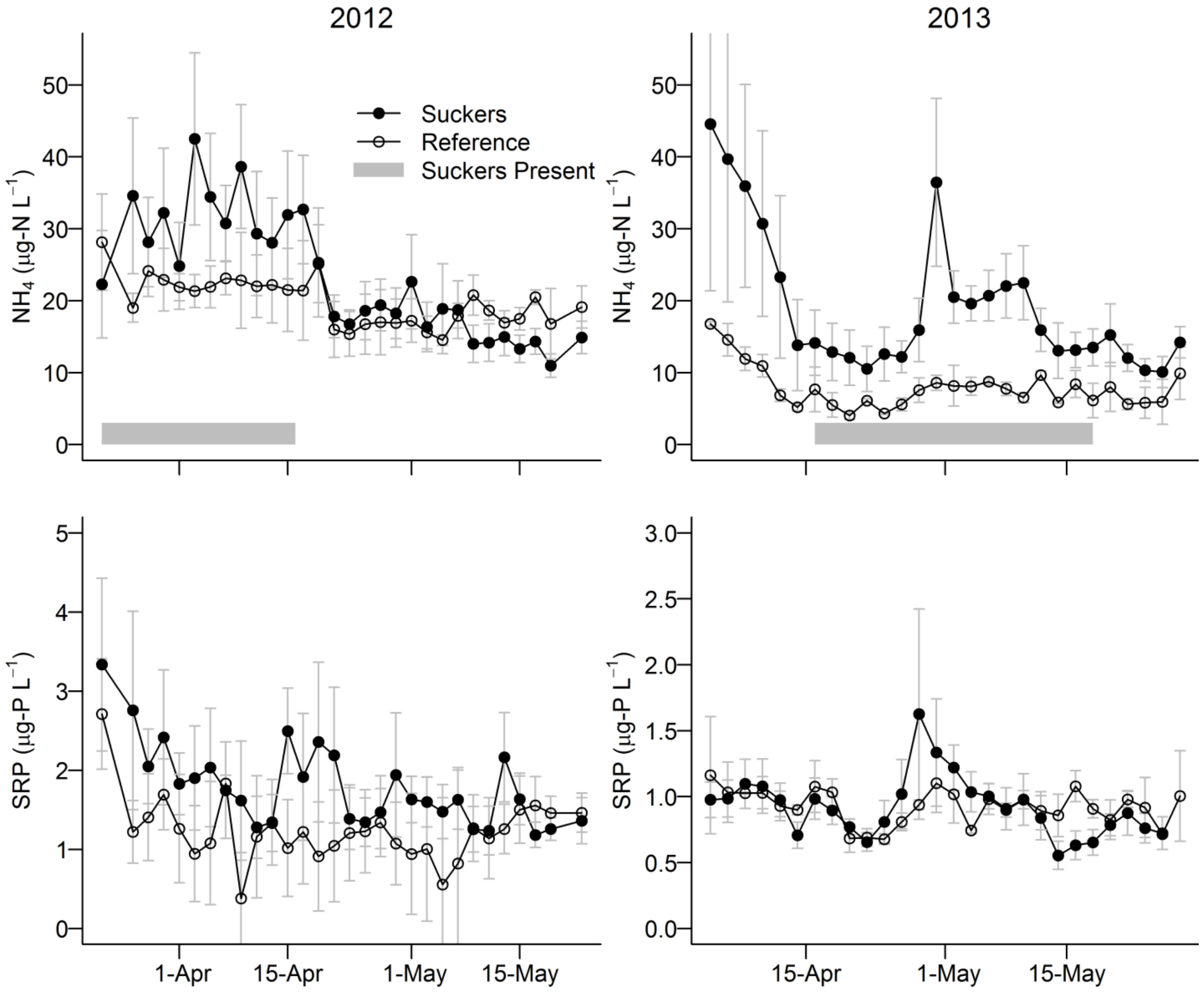

2012
2013
Suckers
Reference
Suckers Present
NH$_4$ (µg-N L^{-1})
SRP (µg-P L^{-1})
0
10
20
30
40
50
0
1
2
3
4
5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
1-Apr
15-Apr
1-May
15-May

Figure 2.

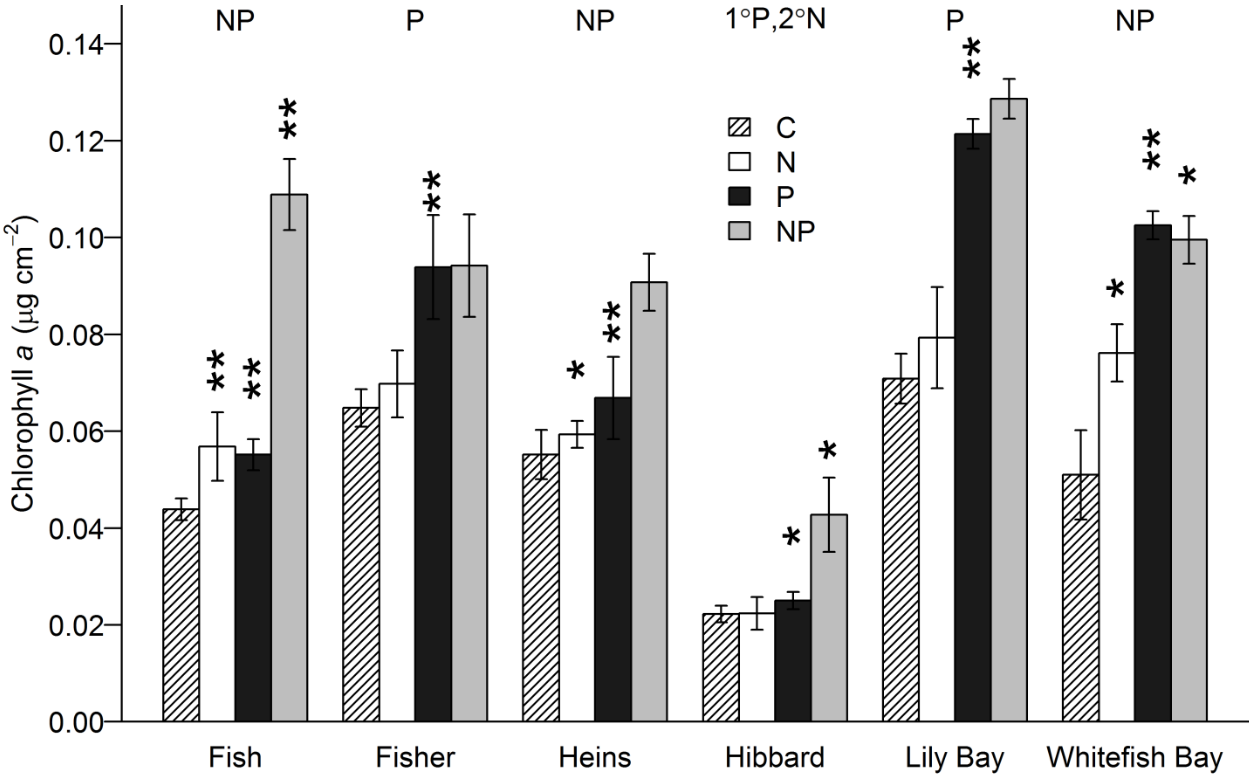

NP
P
NP
1°P,2°N
P
NP
C
N
P
NP
Chlorophyll a (μg cm−2)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Fish
Fisher
Heins
Hibbard
Lily Bay
Whitefish Bay
**
**
**
**
*
**
*
*
**
*
**
*

Figure 3.

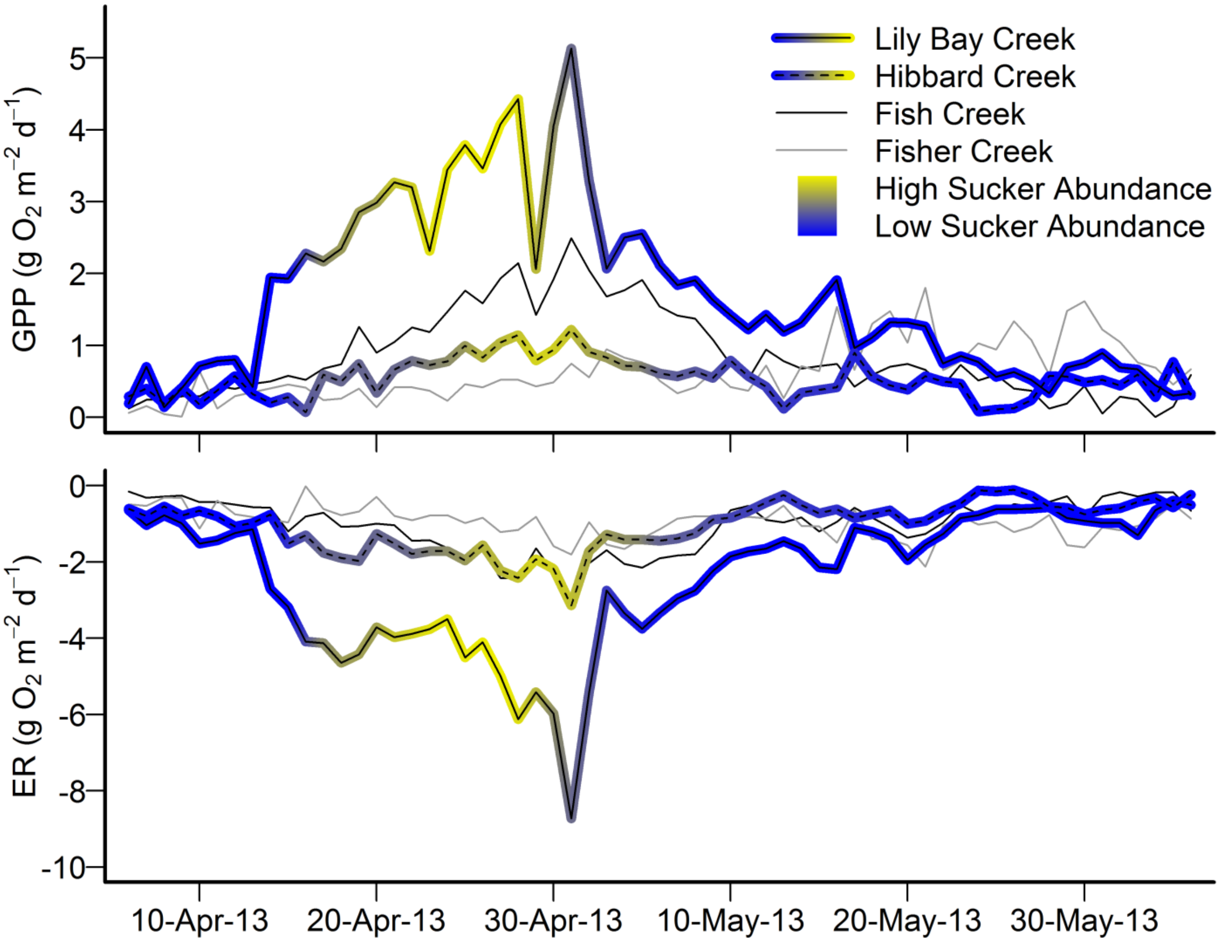

Lily Bay Creek
Hibbard Creek
Fish Creek
Fisher Creek
High Sucker Abundance
Low Sucker Abundance
GPP (g O_2 m^{-2} d^{-1})
5
4
3
2
1
0
ER (g O_2 m^{-2} d^{-1})
0
-2
-4
-6
-8
-10
10-Apr-13
20-Apr-13
30-Apr-13
10-May-13
20-May-13
30-May-13

Figure 4.

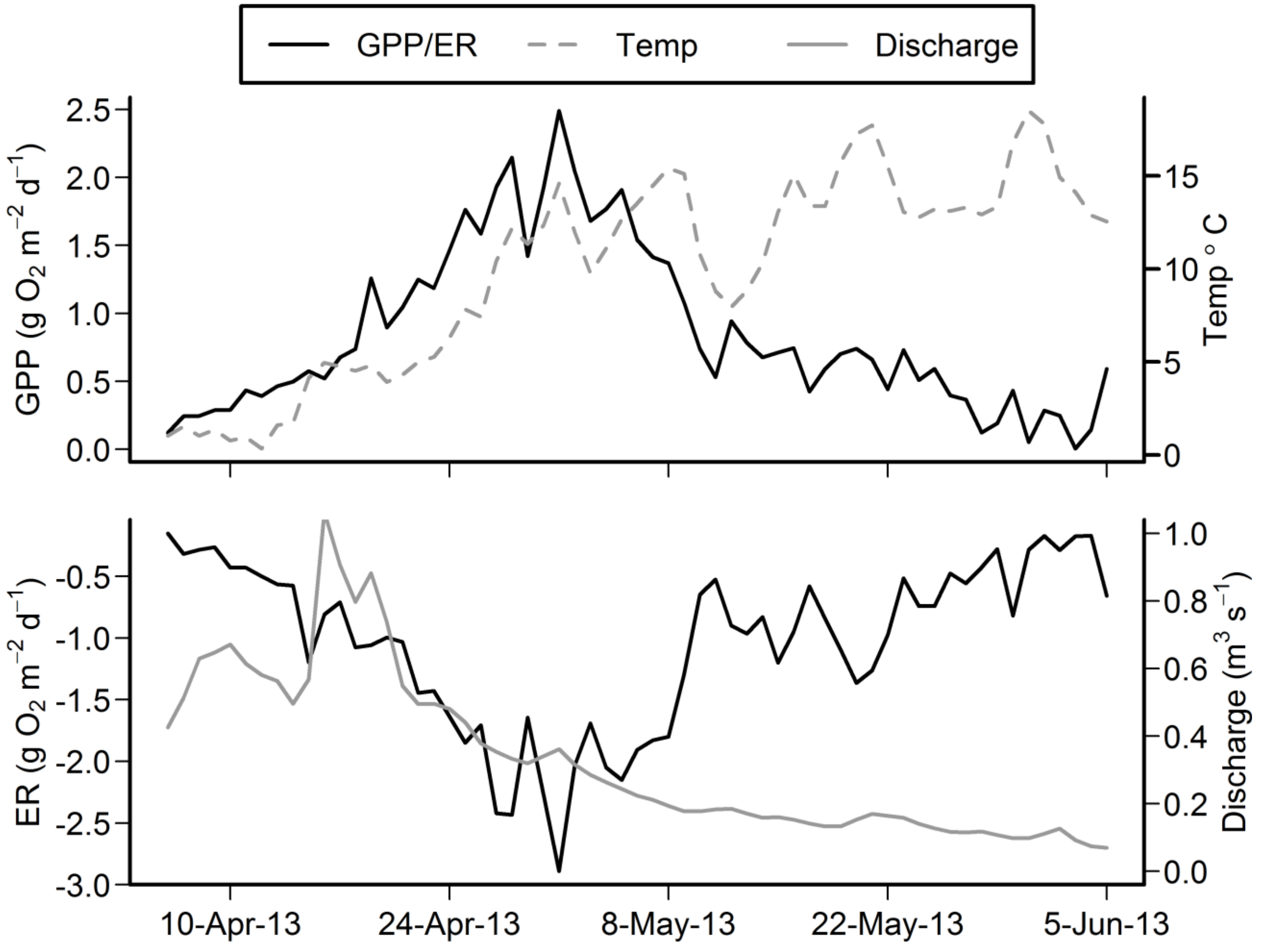
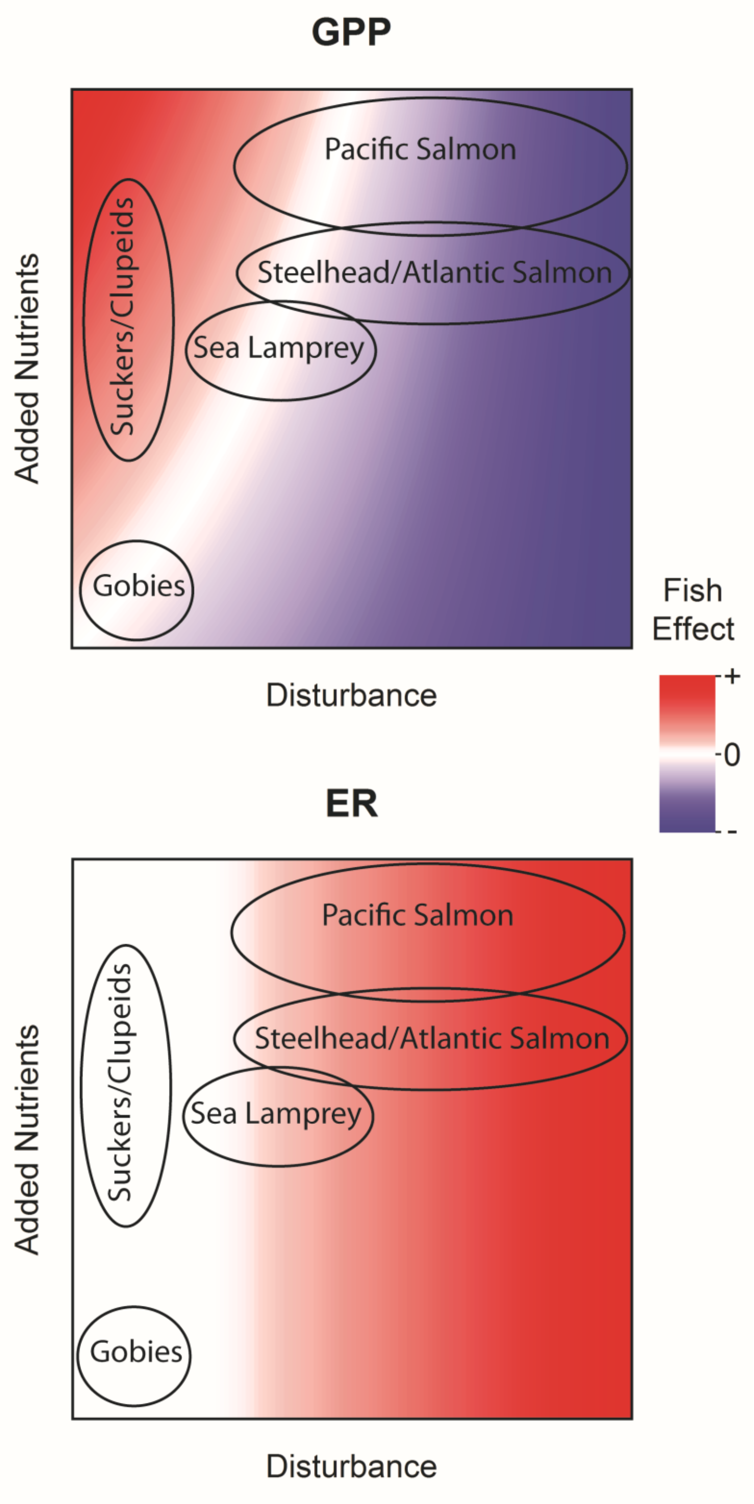

GPP/ER
Temp
Discharge
GPP (g O$_2$ m^{-2} d^{-1})
2.5
2.0
1.5
1.0
0.5
0.0
Temp ° C
15
10
5
0
ER (g O$_2$ m^{-2} d^{-1})
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
Discharge (m^3 s^{-1})
1.0
0.8
0.6
0.4
0.2
0.0
10-Apr-13
24-Apr-13
8-May-13
22-May-13
5-Jun-13

Figure 5.


GPP
Pacific Salmon
Suckers/Clupeids
Steelhead/Atlantic Salmon
Sea Lamprey
Gobies
Added Nutrients
Disturbance
Fish Effect
+
0
-
ER
Pacific Salmon
Suckers/Clupeids
Steelhead/Atlantic Salmon
Sea Lamprey
Gobies
Added Nutrients
Disturbance

Appendix 3.1. Study site details.

Table A1. Study stream attributes. Nutrient concentrations are means over the course of the study.

Site Name	Suckers	Lat.	Long.	SRP (μg-P L^{-1})	NH_4-N (μg-N L^{-1})	NO3-N (μg-N L^{-1})	Baseflow Discharge (L s^{-1})
Fish Creek (Suckers)	Yes	45.126	-87.238	0.6	21	69	99
Fish Creek (Reference)	No	45.125	-87.238	1.0	16	81	99
Fisher Creek	No	44.866	-87.228	1.6	16	1031	58
Heins Creek (Suckers)	Yes	45.012	-87.141	1.9	36	77	155
Heins Creek (Reference)	No	45.017	-87.153	1.3	14	89	155
Hibbard Creek	Yes	44.986	-87.175	1.2	18	1984	199
Lily Bay Creek	Yes	44.848	-87.268	1.7	19	1878	114
Reiboldts Creek	Yes	45.097	-87.082	1.1	33	49	374
Shivering Sands Creek	Yes	44.86	-87.241	1.7	40	533	206
Whitefish Creek	Yes	44.917	-87.224	1.0	10	619	115

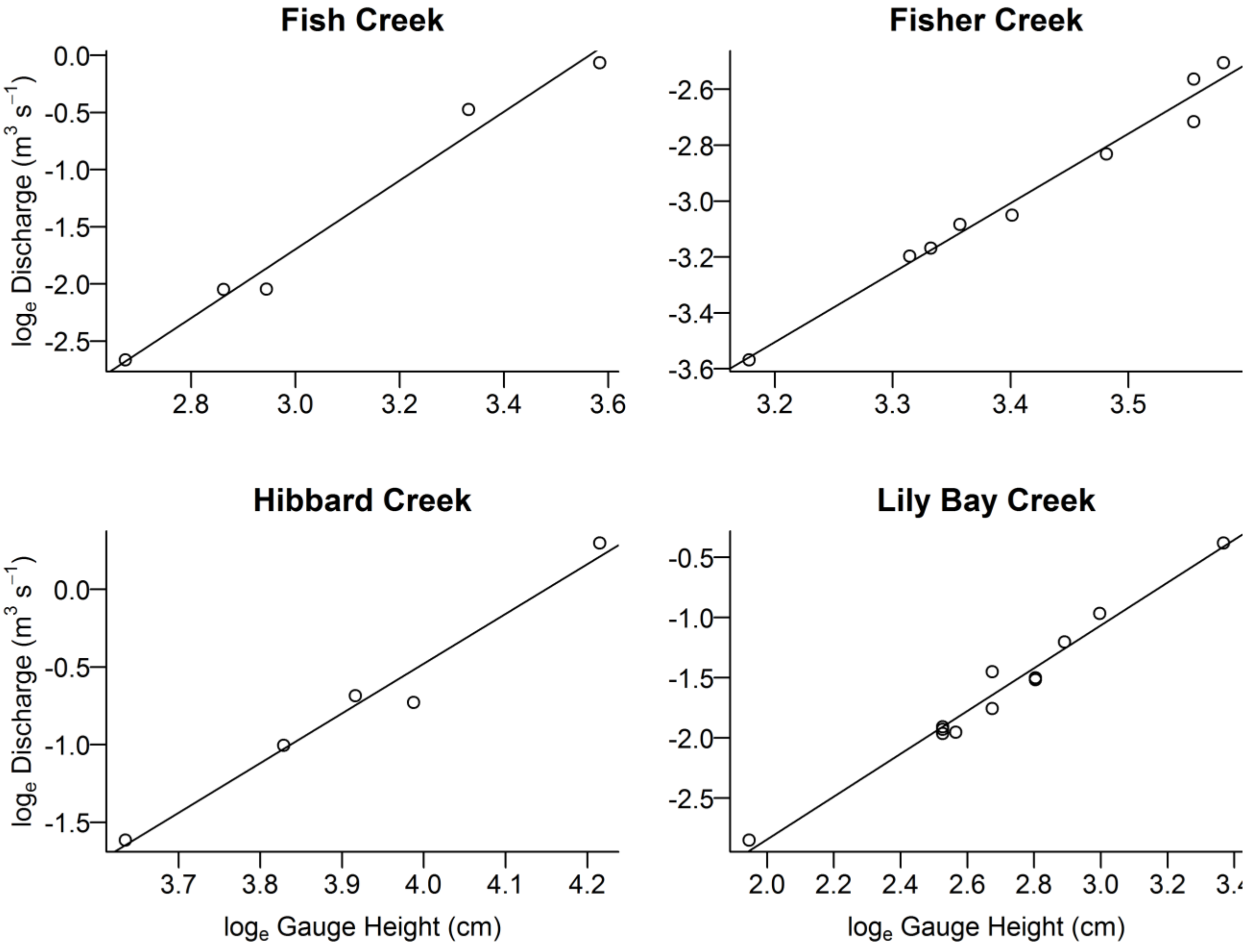


Figure A1. Rating curves used to predict discharge from logged gauge height at each of the four sites where ecosystem metabolism was measured. All $R^2 > 0.97$.

Appendix 3.2

Table A2. Detailed model results for linear mixed effects models of NH_4 concentrations testing for an interaction between whether sites had a sucker migration (SuckerSite) and when suckers were present (SuckersPresent).

NH_4 Fixed Effects

	Estimate	*SE*	*t-value*
Intercept	2.55	0.24	10.5
SuckerSite	0.06	0.11	0.51
SuckersPresent	-0.03	0.09	-0.36
SuckerSite:SuckersPresent	0.34	0.11	3.07

NH_4 Random Effects

Stream	*Intercept*
Fish Creek	2.64
Fisher Creek	2.46
Heins Creek	2.4
Hibbard Creek	2.57
Lily Bay Creek	2.59
Reiboldts Creek	2.8
Shivering Sands Creek	2.86
Whitefish Bay Creek	2.05
sd	0.26

Year	*Intercept*
2012	2.82
2013	2.27
sd	0.29

Residual	
sd	0.56

Table A3. Detailed model results for linear mixed effects models of SRP concentrations testing for an interaction between whether sites had a sucker migration (SuckerSite) and when suckers were present (SuckersPresent).

SRP Fixed Effects

	Estimate	*SE*	*t-value*
Intercept	1.02	0.09	11.83
SuckerSite	0.18	0.05	3.66
SuckersPresent	0.08	0.04	1.85
SuckerSite:SuckersPresent	-0.04	0.05	-0.91

SRP Random Effects

Stream	*Intercept*
Fish Creek	0.88
Fisher Creek	1.2
Heins Creek	1.06
Hibbard Creek	0.93
Lily Bay Creek	1.14
Reiboldts Creek	0.93
Shivering Sands Creek	1.06
Whitefish Bay Creek	0.92
sd	0.12
Year	*Intercept*
2012	1.1
2013	0.93
sd	
Residual	
sd	0.24

Appendix 3.3

Results of nutrient diffusing substrate experiments

Table A4. Results of 2-way ANOVAs testing for the effects of N, P, and their interaction on chlorophyll *a* accrual during nutrient diffusing substrate experiments. A separate 2-way ANOVA was run for each site. The interpretation of each result as nutrient limitation is indicated in the last row.

	Fish Creek		Fisher Creek		Heins Creek		Hibbard Creek		Lily Bay Creek		Whitefish Creek	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
N	**45.1**	**>0.001**	0.03	0.858	**5.6**	**0.028**	3	0.099	1.5	0.23	**4.5**	**0.048**
P	**33.3**	**>0.001**	**10.3**	**0.005**	**13.3**	**0.002**	**5.4**	**0.031**	**61.7**	**>0.001**	**37.4**	**>0.001**
NP	**14.6**	**0.001**	0.1	0.784	2.8	0.112	**4.9**	**0.038**	0.01	0.922	**4.8**	**0.042**
Limitation	NP		P		NP		1°P 2°N		P		NP	

Chapter 4

Stream nutrients integrate signals of current land use and 4-million years of ecosystem development across the Hawaiian archipelago

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To be submitted for publication with co-authors Ernie F. Hain, Benjamin K. Kraemer, James F. Gilliam, Michael J. Blum, and Peter B. McIntyre

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Abstract

Human land use has enhanced nutrient loading to aquatic ecosystems worldwide, but these recent transformations operate against a backdrop of variation in nutrients driven by geochemistry, weathering, and biological nitrogen fixation. The Hawaiian archipelago serves as a model system for ecosystem development due to strong precipitation gradients applied to substrates that are geochemically similar but differ in age by up to 4 million years. The goal of this study was to use stream nutrients to assess the relative influence of current land use and ecosystem development on nutrient availability and losses on the landscape. We analyzed dissolved nitrogen and phosphorus from 113 sites across five islands, and used land cover, soil type, and substrate age data to separate the influence of human land use from background landscape characteristics. Urban development was associated with increased N concentrations and δ^{15}N. In contrast, P concentrations were best predicted by weathering correlates; stream P decreased with substrate age but increased with watershed slope. Our findings indicate that P remains primarily controlled by mineral weathering of P from parent material, which decreases over time but can be renewed through erosion on steep slopes, while N is strongly influenced by human activities. Additionally, decreasing N concentrations and δ^{15}N with soil organic matter indicate that soil nutrient retention and denitrification mediate N losses. Overall, our results

indicate that anthropogenic activities now drive N availability across the Hawaiian archipelago, whereas losses of P during ecosystem development remain a primary control on P availability.

Introduction

Human activities have profoundly increased nutrient availability and altered nutrient cycling globally largely through the use of fertilizers and combustion of fossil fuels (Vitousek et al. 1997, Smil 2000, Asner et al. 2004). Although anthropogenic activities dominate global cycling, these overlie natural variation in nutrient availability due to effects of climate and geology. Natural variation in P is driven by the weathering of P from parent material, which becomes depleted over long periods of time (Walker and Syers 1976). The major natural source of N is biological fixation, so N availability is initially low and increases over time (Hedin et al. 2003). Because human land use has transformed much of the globe, determining the relative influence of ecosystem development and human activities on nutrient availability is necessary for understanding controls on nutrient limitation and productivity. Aquatic ecosystems are particularly vulnerable to changes on the landscape because they integrate processes across their watersheds. Because of this, they also provide valuable information about nutrient losses from the landscape (Bormann and Likens 1967).

Gradients of substrate age and precipitation have proven fruitful for understanding dynamics of nutrient availability in terrestrial ecosystems over the course of ecosystem development (Walker and Syers 1976, Vitousek 2004). Initially, P is locked up in rock but becomes available as the minerals are weathered, eventually becoming depleted in very old soils (Crews et al. 1995). However, in areas with steep slopes, erosion can lead to the exposure of fresh parent material, which can maintain P supplies even in old landscapes (Porder et al. 2005). In contrast, N is derived from the atmosphere through deposition and biological fixation, availability tends to be low on new substrates and higher once fixation and deposition establish N pools (Hedin et al. 2003). However, human domination of global nutrient cycles makes it uncertain as to whether ecosystem development remains a broadly important control on nutrient availability on the modern landscape.

The Hawaiian Islands offer an excellent opportunity to compare the influence of human land use and ecosystem development on nutrient cycling. The formation of the islands as the tectonic plate moved across a volcanic hotspot created a strong gradient of substrate age, ranging from fresh lava flows to substrates over 4 million years old (Wilson 1963). Large elevation change and consistent delivery of moist air by the trade winds also combine to create strong gradients in precipitation (Carlquist 1980). These characteristics make Hawaii a model system for examining the influence of ecosystem development on nutrient cycling (Vitousek 2004). Additionally, land use gradients from high density cities to agricultural lands to virtually uninhabited catchments (Brasher 2003) exist independent of natural gradients in age and precipitation, thereby creating an ideal setting for evaluating the relative contribution of human land use and ecosystem development.

The goal of this study is to determine the relative importance of natural landscape evolution compared to recent human activities for dictating stream nutrient status. Because streams act as integrators of watershed processes, our approach allows inferences about controlling factors across evolving landscapes in general. Across the Hawaiian archipelago, our approach was to combine surveys of stream nutrients and N stable isotopes with watershed data to determine the extent to which current land use overrides historical ecosystem development to control nutrients.

Methods

From June to November of 2009 and March to June 2011, we sampled 113 sites in 39 watersheds across the five Hawaiian Islands with perennial streams (Oahu, Hawaii, Kauai, Maui, and Molokai). Seventy of these sites were sampled in both years. When possible, we sampled three sites separated by >1 km of channel length within each watershed to capture land use and elevation gradients while minimizing variation in other factors. At each site, water samples were filtered (Whatman GD/X, 0.45 um pore) and stored frozen for later analysis of soluble reactive phosphorus (SRP), nitrate (NO_3-N), and ammonium (NH_4-N) using standard colorimetric methods (APHA 1998).

As a potential indicator of N inputs from human sources or biological N-fixation, N stable isotope ratios were measured for three taxonomic groups: algae, snails, and fish. Algal sampling focused on mats of filamentous algae. For snails, samples were collected from the endemic *Neritina granosa* when it was present, and from the non-native *Tarebia granifera* or *Melanoides tuberculata* when it was not. Tissue from 2-4 snails was pooled into a single sample. For fish, samples were collected from the most common of the five native freshwater species, *Awaous stamineus* (Lindstrom et al. 2012). Muscle samples were taken from one large and one small individual at each site (average total length 129 and 92 mm respectively) and kept frozen until they were oven-dried (60ºC, 48hr), ground into a homogeneous powder, and subsampled (1.3 mg) into tin capsules for analysis of stable isotope ratios N at the Cornell University Stable Isotope Laboratory. Results are expressed using standard δ^{15}N notation, and analytical precision for trout muscle standards interspersed periodically throughout our samples was 0.11‰ (SD, n=16) and 0.13‰ (n=17). There was no difference in stable isotope ratios between large and small *A. stamineus* (paired t-test: t = 1.51, $P = 0.14$, average difference = 0.15‰), so the average of the two was used in further analysis.

To evaluate the influence of land cover on stream nutrients, land use statistics were derived from the 2001 National Land Cover Database (Homer et al. 2007), which was the most recent land use data available for Hawaii, using ArcGIS (ArcGIS Desktop: Release 9.3, ESRI, Redlands CA, USA). The proportion of each land cover type was determined for the upstream catchment of each sampling location. Urban development, forest, grassland, wetland, crop, and pasture were evaluated for influence on stream nutrient chemistry.

A suite of geological and ecosystem properties were determined for the upstream catchment of each site to examine their influence on stream nutrient concentrations, including soil organic matter (SOM) content, substrate age, precipitation, and watershed slope (See Table A1 for island and watershed summaries). SOM was estimated using the Soil Survey Geographic Database (USDA 2014), which includes the spatial distribution of soil types with direct measurements of soil properties. SOM was calculated as the product of percent organic matter and bulk density integrated over the soil profile, which yielded an estimate of mass of SOM per area. Proportional representation of soil types in each site catchment was estimated in ArcGIS and used to calculate the area-weighted average SOM for each catchment. A similar approach was used to estimate substrate average age. Substrate age ranges for each substrate type were derived from a state geologic map (Sherrod et al. 2007), and watershed age was estimated by taking the median age for each substrate type and calculating the area-weighted average substrate age for the watershed. Watershed precipitation was obtained from the Hawai'i rainfall atlas (Giambelluca et al. 2013), and watershed slope was derived from 10 m resolution digital elevation maps (Gesch et al. 2002).

Linear mixed-effects models were used to examine influence of landscape characteristics on SRP, NH_4, NO_3, and $\delta^{15}N$. An information-theoretic approach was used to evaluate possible models and determine the importance of variables as predictors. All possible combinations of predictors were fit using mixed-effects models with random intercepts for watershed, island, and year to account for non-independence of samples within these categories using the lme4 package in R (R Core Team 2014). Interactions among pairwise combinations of age, precipitation, and watershed slope were included as possible predictors but only in models containing the main effects of interacting variables. Variance inflation factors were used to evaluate co-linearity among the predictors. All predictors had a VIF < 3, except watershed slope, which had VIF = 4. Models were selected on the basis of Akaike's information criterion with small-sample correction (AICc), and we will henceforth refer to the model with the lowest AICc as the best model. Models within 2 AICc of the best model were retained, and averaging of these top models was used to estimate slopes and importance for predictors using Akaike weights (Johnson and Omland 2004). Prior to analyses, land cover metrics were arcsine-square root transformed prior to analyses, and substrate age, watershed area, precipitation, and nutrients were log transformed. Standard scores of predictors were used in analyses; however, direct comparison of coefficients is still complicated by transformations. Marginal and conditional R^2 values were used to assess the goodness of fit for the full model and the model with the lowest AICc. Marginal R^2 (R^2_m) represents the proportion of variation explained by the fixed effects, while conditional R^2 (R^2_c) represents the variation explained by the fixed effects and random effects together (Nakagawa and Schielzeth 2013).

Results

Landscape Influences on Nitrogen

NO_3 varied from <1 μg-N L^{-1} to over 1000 μg-N L^{-1} across the study sites with a median of 10 μg-N L^{-1}. The highest average concentrations were on Oahu (162.0 μg-N L^{-1}), the most developed island, and the lowest on Molokai (8.5 µg-N L^{-1}), the least developed island. Across all sites, NO_3 averaged 55.7 µg-N L^{-1} (SD = 202.6), and the ranges of NO_3 overlapped for all islands. AICc weights identified urban development, crops, SOM, and watershed slope as the most important predictors of NO_3 (Fig. 1). NO_3 increased with urban development and crops but decreased with increasing SOM (Fig. 2). Both the full and best models explained a large proportion of the variation in NO_3, however much of this was partitioned into the watershed random effect (full model: $R^2_m = 0.36$, $R^2_c = 0.72$; best model: $R^2_m = 0.30$, $R^2_c = 0.72$).

NH_4 averaged 11.3 µg-N L^{-1} (SD = 9.9) across all sites with the highest concentrations on Oahu (16.6 µg-N L^{-1}) and Kauai (13.0 µg-N L^{-1}) and lower concentrations on Molokai (9.8 µg-N L^{-1}), Maui (7.7 µg-N L^{-1}), and Hawaii (7.2 µg-N L^{-1}), but ranges overlapped for all islands. AICc weights identified catchment area and precipitation as the most important predictors of NH_4 (Fig. 1); however the best model also included substrate age and SOM. For both the full model and the best model, the fixed effects only explained a small proportion of the variance (full model R^2_m = 0.21, best model R^2_m = 0.19), and variance was partitioned to both the island and year random effects (full R^2_c = 0.38, best R^2_c = 0.35).

There was high variability in $\delta^{15}N$ across the sites for all taxa (*A.stamineus* range: 2.8 to 17.3‰, snails: 1.5 to 14.4‰, and algae: -1.7 to 14.2‰). There was strong concordance among $\delta^{15}N$ for algae, snails, and fish from the same site. Linear regressions among $\delta^{15}N$ for the taxa were all significant ($P < 0.001$) and described a large proportion of the variation (snail vs algae: $R^2 = 0.80$; *A. stamineus* vs algae: $R^2 = 0.82$; *A. stamineus* vs snail: $R^2 = 0.83$). Taxa differed consistently in $\delta^{15}N$ across sites; *A. stamineus* were an average of 2.5‰ (SD = 1.2) higher than snails, and snails were an average of 2.4‰ (SD = 1.4) higher than algae. $\delta^{15}N$ was also correlated with dissolved inorganic N (linear regression for *A. stamineus*: $R^2 = 0.42$, $P < 0.001$).

From the LME model selection, the most important landscape predictors for $\delta^{15}N$ were fairly consistent across taxa; $\delta^{15}N$ of all taxa increased with urban development and substrate age and decreased with increasing SOM (Fig. 2, Fig. 3). The fixed effects in LME models for snail $\delta^{15}N$ explained the largest proportion of the variance (full model: $R^2_m = 0.76$, $R^2_c = 0.82$, best model: $R^2_m = 0.73$, $R^2_c = 0.81$), followed by the models for *A. stamineus* $\delta^{15}N$ (full model: $R^2_m = 0.73$, $R^2_c = 0.94$, best model: $R^2_m = 0.71$, $R^2_c = 0.94$), and the algal $\delta^{15}N$ models explained the smallest proportion of the variance (full model: $R^2_m = 0.69$, $R^2_c = 0.82$; best model: $R^2_m = 0.64$, $R^2_c = 0.82$). For all taxa, variation was partitioned to the watershed random effect, and year also explained variation in algal $\delta^{15}N$.

Landscape Influences on Phosphorus

SRP averaged 8.4 µg-P L^{-1} (SD = 6.6) across all sites and Molokai, the least developed island, had the highest mean concentration (12.5 µg-P L^{-1}). Average concentrations on the other four islands ranged between 6.5 and 8.5 µg-P L^{-1}, but the ranges for all islands overlapped. Substrate age and watershed slope were identified as the most important predictors of SRP in the model selection and were contained in all of the preferred models (Fig. 1). In both the full and best models for SRP, the fixed effects explained more variation than the dissolved N models (full: $R^2_c = 0.46$, best: $R^2_c = 0.40$). Further variation was explained by the watershed, island, and year effects (full: $R^2_m = 0.75$, best: $R^2_m = 0.66$), with the largest proportion explained by watershed.

Landscape Influences on N:P

The molar ratio of dissolved inorganic N to SRP varied from <1 to >300. There was substantial overlap among the ranges of N:P for islands, but the lowest values occurred on Hawaii, which is youngest island, and the highest values occurred on Kauai and Oahu, the oldest and most developed islands respectively. The most important variables in LME models of N:P were substrate age, soil organic matter, and cropland (Fig. 1), which explained around a third of the variation (full model: $R^2_m = 0.36$; best model: $R^2_m = 0.32$). Watershed and year effects explained further variation in N:P ($R^2_c = 0.56$, $R^2_c = 0.56$).

Discussion

Anthropogenic land use, ecosystem development, and physical watershed properties all affected the nutrient status of Hawaiian streams, shifting the balance of N and P across the archipelago. P concentration was most strongly related to factors associated with physical weathering: substrate age and watershed slope. In contrast, NO_3 concentrations were most strongly associated with anthropogenic land use and SOM. NH_4 was not well explained by the models, which is likely due to other forms of N dominating watershed loss (Houlton et al. 2006) or the dynamic nature of this N fraction. Overall, we found that background ecosystem properties interact with human land use to influence nutrient availability in Hawaiian streams; weathering was the primary influence on P, whereas human land use and soil properties were most important for N.

Anthropogenic sources of N appear to be an important source of N but not P. NO_3 and $\delta^{15}N$ increased with urban development, which is consistent with widespread findings that urbanization increases nutrient concentrations in continental (Allan 2004) as well as tropical island settings (Ramírez et al. 2009). The watershed with the highest urban development were outliers in NO_3 and $\delta^{15}N$, having moderate values for both. This stream is entirely channelized and mostly contained in a covered concrete channel, which may reduce its interaction with the surrounding urban landscape. Crops in the upstream watershed also had a positive effect on NO_3 concentrations, likely through the application of inorganic fertilizers and/or the planting of biological N-fixers. N stable isotopes are often used as indicators of anthropogenic nitrogen contributions to aquatic ecosystems (Anderson and Cabana 2006, Bergfur et al. 2009, Diebel and Vander Zanden 2009) including Hawaiian coastal wetlands (Bruland and MacKenzie 2010). Anthropogenic N inputs tend to increase N isotopic ratios through either high-δ^{15}N sources or enhanced N processing (Robinson 2001, Hastings et al. 2013).

SOM was also an important predictor of stream N. These relationships were clear despite the fairly course calculation of SOM across the landscape. We extrapolated SOM measurements from soil surveys using soil type, which ignores the spatial variability within soil type due to precipitation, vegetation, or transport. Still, the relationships between SOM and N were clear, suggesting that there is a robust connection between the two. The decreasing N concentrations with increasing SOM were likely driven by the high nitrogen retention capacity of organic rich soils (Fenn et al. 1998) and the dependence of denitrification on the presence of labile organic carbon (Zech et al. 1997). Higher organic matter content is associated with increased microbial uptake and increased cation exchange capacity, which can drive high nutrient immobilization (Johnson 1992). Additionally, the presence of labile carbon contributes to favorable conditions for denitrification, and high demand for NO_3 reduces isotopic fractionation leading to lower soil δ^{15}N (Houlton et al. 2006). Variability in denitrification is a major source of variation in Hawaiian soil δ^{15}N (Houlton et al. 2006). Thus, decreasing NO_3 and δ^{15}N with increasing SOM is most likely driven by higher gaseous losses, which reduce both total loss and isotopic fractionation.

Although land use and SOM had clear effects on N, weathering-related variables were more important for P. Our finding that SRP concentrations decreased with substrate age is consistent with losses through weathering during ecosystem development (Crews et al. 1995, Chadwick et al. 1999). Weathering of rocks is the primary source for P in natural ecosystems (Smil 2000) and highly weathered materials decrease in P content, leading to lower P losses from older substrates. Similarly, the strong positive relationship between P and watershed slope is likely driven by erosion, which increases with slope, exposing new parent material and providing phosphorus to the ecosystem (Porder et al. 2005). Thus, weathering of P from parent material appears remain an important determinant of nutrient availability even in the context of human land use.

Differing controls on N and P across the landscape led to highly variable N:P ratios. The relationships of N with both human land use and SOM translated to lower N:P ratios, while decreasing P with substrate age led to higher N:P ratios. Thus, the distinct controls on N and P shift the balance of nutrients and probably nutrient limitation along gradients of human land use and ecosystem development. Ecosystems are generally thought to shift from N to P limitation along the trajectory of ecosystem development as P is weathered from rocks and N accumulates (Vitousek and Farrington 1997). Our results suggest that anthropogenic N sources may accelerate this transition in nutrient limitation across the Hawaiian archipelago.

Landscape attributes explained larger proportions of the variation in SRP and δ^{15}N than in NO_3, and very little of the modest variation in NH_4 was explicable. Nitrogen is more mobile than P in the atmosphere and on the landscape (Vitousek et al. 2010). Locally, industrial and volcanic activity as well as wastewater treatment plants can be sources for atmospheric N (Huebert et al. 1999, Vymazal 2007), but N from Asia and North America is also a major source of N deposited in the Hawaiian islands (Carrillo et al. 2002). In spite of the importance of larger scale processes (Chadwick et al. 1999), we found that most of the variation in N and P was explained at the watershed scale indicating that streams were effective sentinels for landscape-scale variability. $\delta^{15}N$, in particular was strongly related to landscape variation, and because $\delta^{15}N$ of deposition in Hawaii is similar to fixation (Houlton et al. 2006), watershed-scale variation in N cycling appears to be the dominant control on $\delta^{15}N$.

Although most research on nutrient cycling in the Hawaiian archipelago has focused on ecosystem development, our results demonstrate that these processes interact with human land use to influence nutrient availability in streams. In particular, human land use has altered N availability across the Hawaiian landscape, but weathering of parent material remains a strong landscape control on P.

Acknowledgements

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Figure Captions

Figure 1. Results of linear mixed model averaging for models within 2 AICc of the best model for stream nutrient concentrations across the Hawaiian archipelago. Error bars for coefficients indicate 95% confidence interval. Filled circles indicate coefficients whose confidence interval does not overlap with zero. Bolded variables were contained in the model with the lowest AICc.

Figure 2. Univariate relationships of NO_3 and $\delta^{15}N$ with urban development and soil organic matter in the watershed.

Figure 3. Results of linear mixed model averaging for models within 2 AICc of the best model for $\delta^{15}N$ of biota across the Hawaiian archipelago. Error bars for coefficients indicate 95% confidence interval. Filled circles indicate coefficients whose confidence interval does not overlap with zero.

Figure 4. Soluble reactive phosphorus concentrations in streams across a gradient of substrate age.

Figure 1.

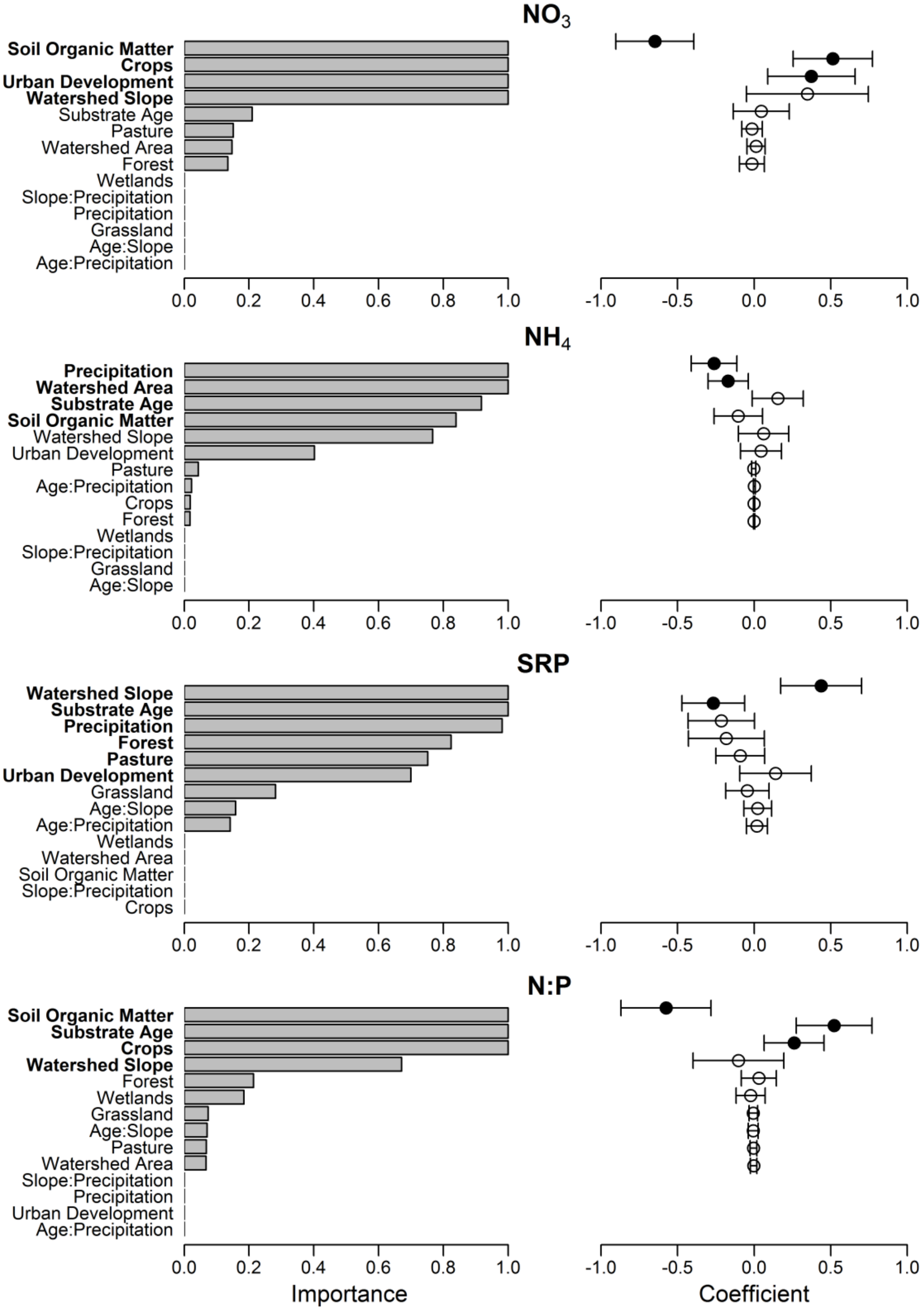
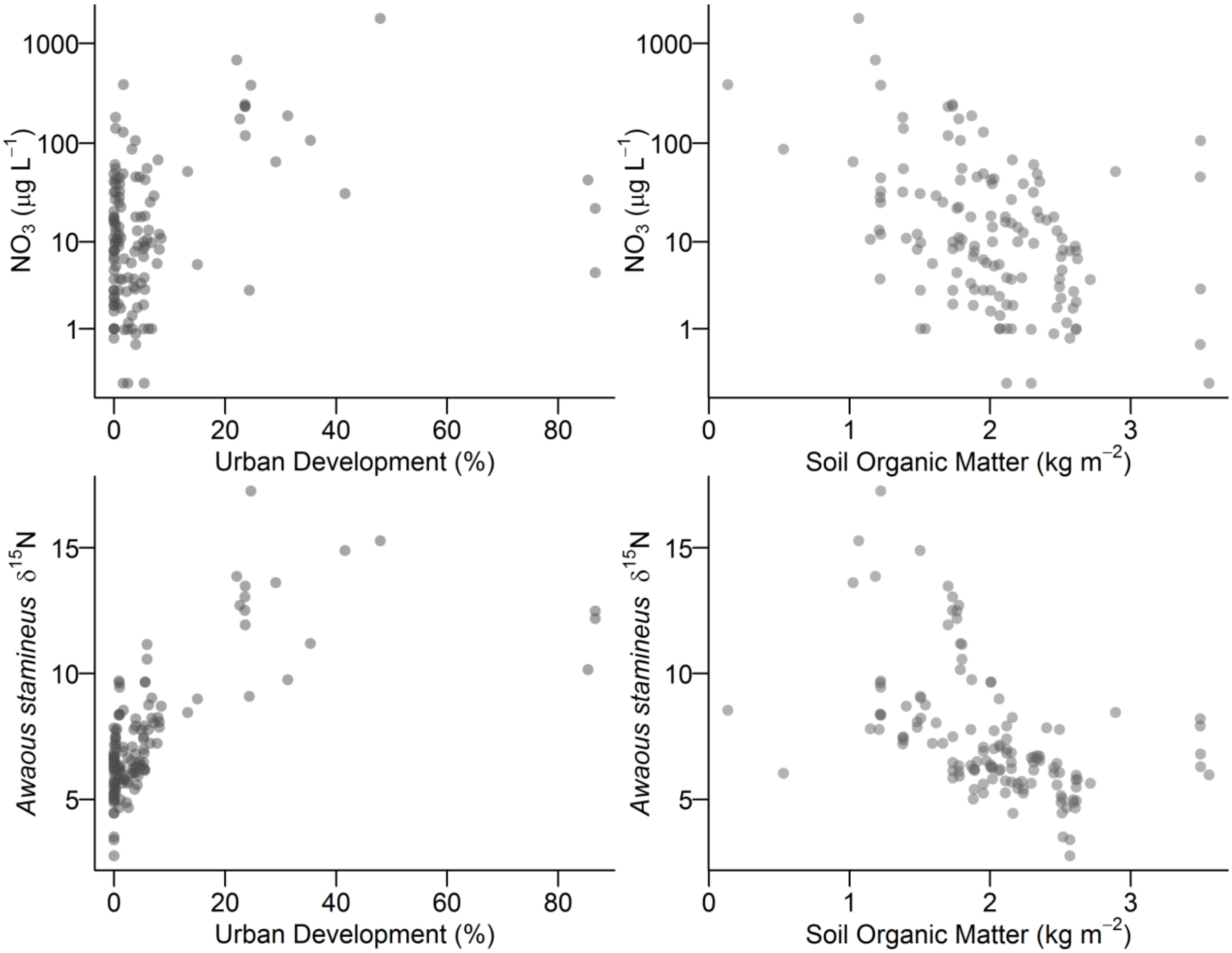
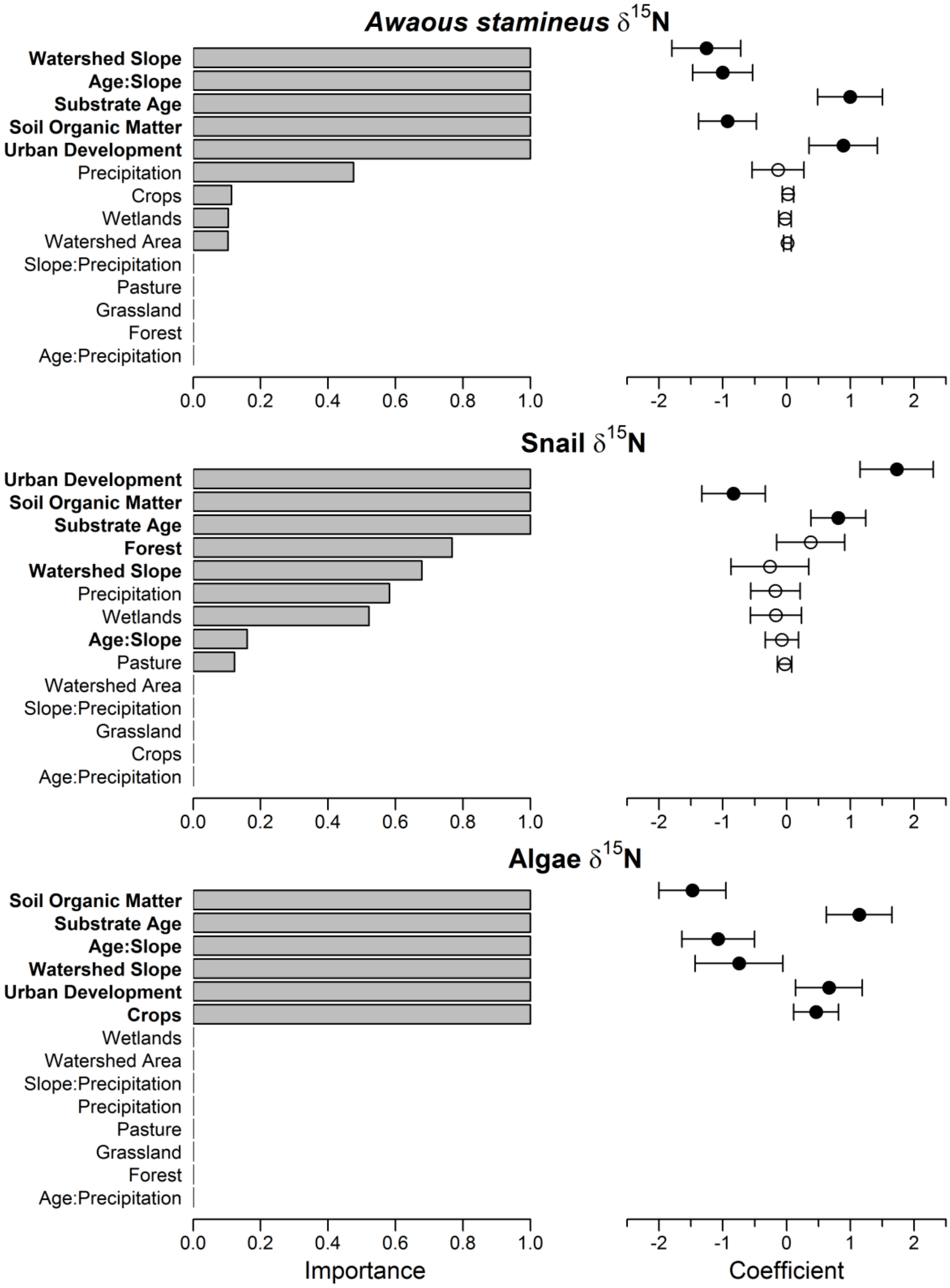

NO$_3$
Soil Organic Matter
Crops
Urban Development
Watershed Slope
Substrate Age
Pasture
Watershed Area
Forest
Wetlands
Slope:Precipitation
Precipitation
Grassland
Age:Slope
Age:Precipitation
NH$_4$
Precipitation
Watershed Area
Substrate Age
Soil Organic Matter
Watershed Slope
Urban Development
Pasture
Age:Precipitation
Crops
Forest
Wetlands
Slope:Precipitation
Grassland
Age:Slope
SRP
Watershed Slope
Substrate Age
Precipitation
Forest
Pasture
Urban Development
Grassland
Age:Slope
Age:Precipitation
Wetlands
Watershed Area
Soil Organic Matter
Slope:Precipitation
Crops
N:P
Soil Organic Matter
Substrate Age
Crops
Watershed Slope
Forest
Wetlands
Grassland
Age:Slope
Pasture
Watershed Area
Slope:Precipitation
Precipitation
Urban Development
Age:Precipitation
0.0
0.2
0.4
0.6
0.8
1.0
-1.0
-0.5
0.0
0.5
1.0
Importance
Coefficient

Figure 2.



NO_3 (μg L^{-1})
1000
100
10
1
0
20
40
60
80
Urban Development (%)
NO_3 (μg L^{-1})
1000
100
10
1
0
1
2
3
Soil Organic Matter (kg m^{-2})
Awaous stamineus $\delta^{15}N$
15
10
5
0
20
40
60
80
Urban Development (%)
Awaous stamineus $\delta^{15}N$
15
10
5
0
1
2
3
Soil Organic Matter (kg m^{-2})

Figure 3.


Awaous stamineus δ^{15}N
Watershed Slope
Age:Slope
Substrate Age
Soil Organic Matter
Urban Development
Precipitation
Crops
Wetlands
Watershed Area
Slope:Precipitation
Pasture
Grassland
Forest
Age:Precipitation
0.0
0.2
0.4
0.6
0.8
1.0
-2
-1
0
1
2
Snail δ^{15}N
Urban Development
Soil Organic Matter
Substrate Age
Forest
Watershed Slope
Precipitation
Wetlands
Age:Slope
Pasture
Watershed Area
Slope:Precipitation
Grassland
Crops
Age:Precipitation
0.0
0.2
0.4
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-2
-1
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1
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Algae δ^{15}N
Soil Organic Matter
Substrate Age
Age:Slope
Watershed Slope
Urban Development
Crops
Wetlands
Watershed Area
Slope:Precipitation
Precipitation
Pasture
Grassland
Forest
Age:Precipitation
0.0
0.2
0.4
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Importance
-2
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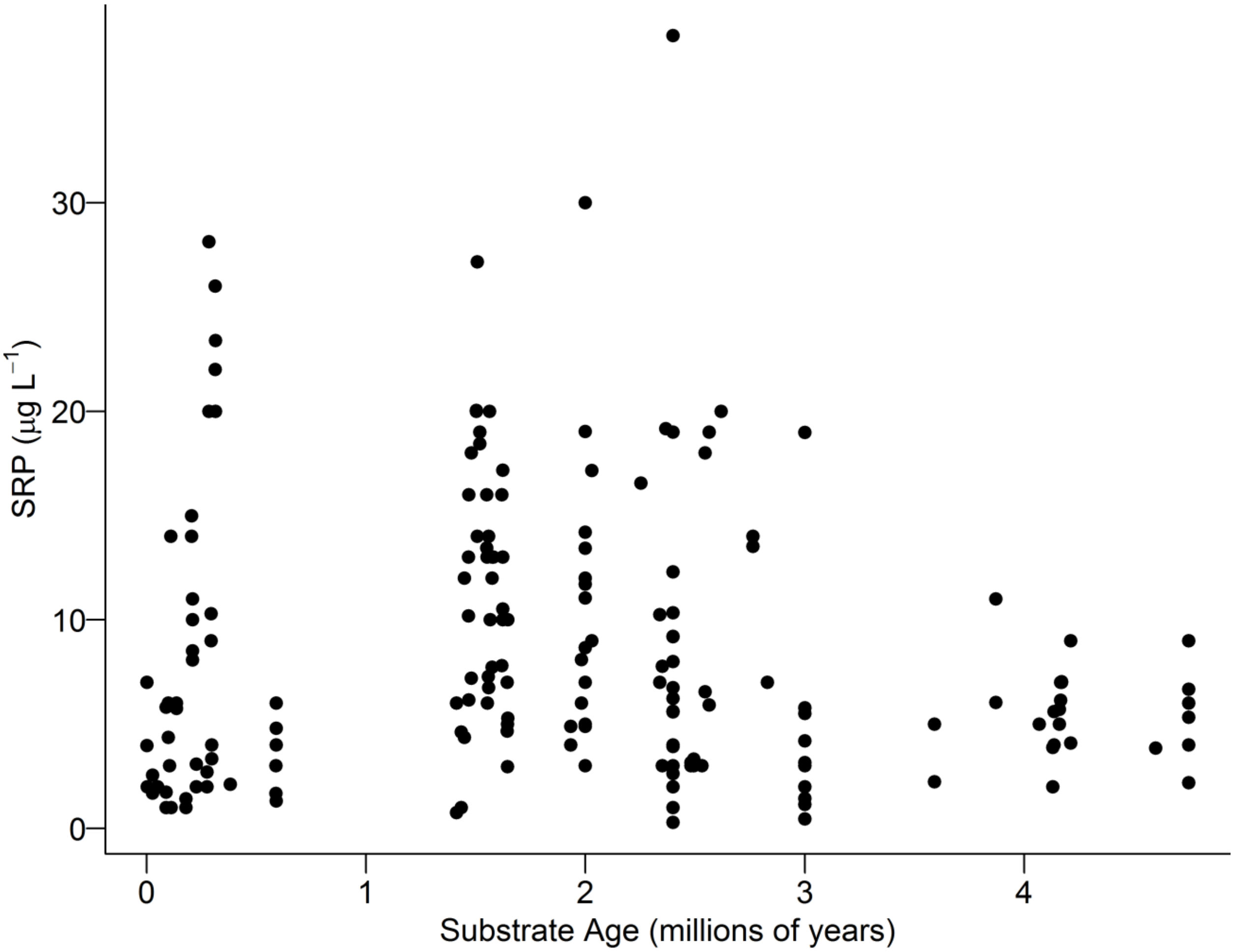
Coefficient

Figure 4.



Appendix 4.1

Table A1. Watershed and island characteristics for variables evaluated as predictors of Hawaiian stream nutrient chemistry.

Stream	% Urban Development	% Forest	% Pasture	% Crop	% Wetland	% Grassland	Substrate Age (10^6 yrs)	Precipitation (mm yr^{-1})	Watershed Slope	Soil Organic Matter (kg m^{-2})
Hawaii	**4.8**	**61.3**	**11.2**	**2**	**0**	**7.7**	**141**	**3842**	**10.5**	**23.9**
Hakalau	1.7	63.4	2.7	0.9	0	16.1	27	4287	8.5	26.5
Honoli'i	5.4	75.6	4.3	5.5	0	2.1	91	5468	6.9	25.1
Kaieie	19.7	26.3	34.4	6.9	0	0.6	75	4615	7.7	17.8
Nanue	1.1	90.2	3.3	0.7	0	0	109	5514	9.1	36.4
Niuli'i	5.2	76.2	7.2	0	0	1.6	209	2432	10	21.2
Wai'ula'ula	5.8	24.6	36.9	0.2	0	20.2	213	1483	9.4	29.7
Wailoa (Waipio)	0.7	63.5	3.5	0.7	0	15.6	304	3016	24.2	15.7
Wailoa River	1.6	40.5	0.2	0.7	0	0.3	2	3227	4.6	1.3
Kauai	**7.7**	**56.8**	**0**	**0.9**	**3.2**	**5.7**	**3497**	**2646**	**23.4**	**17.9**
Hanakäpï'ai	0	74.8	0	0	0.2	0.1	4750	3249	33.8	23.6
Hanapëpë River	1.5	58.8	0	2.5	0.1	5.7	4069	2942	29.5	18.1
Kapa`a	3.9	57.1	0	0.8	0.2	4.8	3891	2864	24.1	19.4
Läwa'i	15.7	59.6	0	0.5	1	4.3	2712	2330	18.6	18.4
Moloaa	8.2	50.6	0	0.5	0.6	13.9	2482	1890	14.2	14.8
Näwiliwili	29	38.7	0	5.6	0.8	9.4	2000	1628	9.2	14.7
Waimea	0.9	44.6	0	0	11.2	8.7	4142	1990	26.3	12.2
Wainiha	1.1	62.6	0	0	10.3	0.8	4600	4305	33.7	20.1

Table A1 Continued.

Stream	% Urban Development	% Forest	% Pasture	% Crop	% Wetland	% Grassland	Substrate Age (10^6 yrs)	Precipitation (mm yr^{-1})	Watershed Slope	Soil Organic Matter (kg m^{-2})
Maui	**1.6**	**59.7**	**0**	**0.2**	**2**	**3.3**	**1381**	**3753**	**34.4**	**22.8**
Alelele	0.1	97.3	0	0	0.4	0.2	591	4609	21.9	23.1
Honoköhau	2.7	76.5	0	0.5	3.1	0.3	1562	4023	36.1	25.5
Iao	1.3	58.5	0	0.4	0.3	1.3	1645	4446	40.1	25.6
Kahakuloa	2.5	78.5	0	0	7.2	3.8	2000	2847	31.1	22.9
Piinaau	0.9	58.6	0	0	0	3.1	382	3536	18.2	17.4
Ukumehame	0.7	27.4	0	0	0	15.7	2000	1819	44.2	11.4
Waihe'e River	2	34.1	0	0.3	3.9	2.5	1742	3968	41.1	25.6
Molokai	**0.1**	**67.8**	**0**	**0**	**0**	**4.6**	**1578**	**2670**	**29.6**	**22.4**
Halawa	0	79.2	0	0	0	1.1	1432	2682	22.5	19.5
Honouli Wai	0.1	61.8	0	0	0	7.1	1472	2386	23.8	21.3
Pelekunu	0	54.2	0	0	0	6.7	1873	2702	40.5	25.5
Waikolu	0.2	58.5	0	0	0	6.1	1510	2622	34	21.9
Wailau	0	87.4	0	0	0	1.1	1600	3053	32.8	23.8
Oahu	**17.4**	**62.3**	**0**	**0.2**	**0.1**	**0.2**	**2501**	**3188**	**27.3**	**16.7**
Ala Wai	24.9	66.8	0	0	0	0	1982	3112	27.3	19.4
Anahulu River	0.6	93.6	0	0	0	0	2400	4445	27	26.1
Kahaluu	40.7	39.7	0	0	0	0	3000	1969	20.8	14.9
Kahana	5.1	76	0	0	0	0	2400	5306	32.3	18.8
Kaluanui	4	75.7	0	0.1	0	0.3	3000	3607	33.4	18.3
Kea'ahala	61.1	19.9	0	0	0	0	2461	1992	15.3	14.6
Waiahole	6	54.4	0	0	0	0	2550	3508	32.7	10.9
Waikäne	7.1	78.4	0	0	0	0.1	2400	3319	30.8	16.2
Waimea	2.4	91.1	0	0	0	0	3000	3018	25.9	22.5
Waimea River	2.9	89.9	0	0	0	0.5	2400	2751	25.4	20.9
Waimänalo	31.6	51	0	2	0.1	0	2363	1659	19.2	11.6