ARTICLE

Impacts of Adfluvial Fish on the Ecology of Two Great Lakes Tributaries

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Abstract

Anadromous and adfluvial fish can transport high concentrations of nutrients and energy into streams during spawning runs. While the ecological effects of their spawning migrations are variable, in some instances these fish contribute to increased nutrient concentrations, primary productivity, invertebrate biomass, and resident fish growth and survival in the nutrient-poor streams of the Pacific Northwest. In tributaries of the Great Lakes, the effects of introduced salmonid and native adfluvial fish are poorly documented. We conducted field experiments to determine the effects of a semelparous fall fish, Chinook salmon *Oncorhynchus tshawytscha*, and an iteroparous spring fish, steelhead *O. mykiss*, on the ecology and productivity of two tributaries to the Muskegon River, Michigan, a Lake Michigan tributary. We sampled stream biota and water chemistry before and after the introduction of Chinook salmon carcasses and eggs in the fall and steelhead eggs in the spring in a tributary stream with natural spawning runs and in another tributary stream without runs but with carcass and egg additions. There was no response in terms of invertebrate density or water chemistry to spawning migrations or salmon carcass introductions in either tributary. The density of resident brown trout *Salmo trutta* increased in both stream types after the introduction of salmon carcasses in the fall, and energy consumption increased after the addition of salmon eggs in the fall and spring in the manipulated stream. Based on stomach content analysis, fish that had eggs in their stomachs also consumed more energy than fish that did not consume eggs. The results suggest that adfluvial fish may affect some tributaries of the Great Lakes by providing high-energy food sources to resident stream fish, but the potential effect of this egg consumption on resident fish growth and survival requires more research.

Fish transport nutrients and increase primary productivity in aquatic ecosystems through a variety of mechanisms. In lakes, fish transport nutrients predominately through excretion (Kraft 1993; Vander Zanden and Vadeboncoeur 2002; Vanni 2002). In rivers, fish play a prominent role in transporting nutrients into streams during extensive spawning runs, as exemplified by spawning Pacific salmon in the Pacific Northwest (Gende et al. 2002) and suckers in the Great Lakes (Burtner 2009; Childress 2010; Flecker et al. 2010). As anadromous and adfluvial fish move during their spawning runs they transport

TABLE 1. Comparison of nutrient concentrations among various streams in Alaska, British Columbia, and the Great Lakes. Ranges were determined for British Columbia by combining three streams and 3 years studied by Johnston et al. (2004; Figure 6), assuming that the first date of measurement had no salmon and that the peak included salmon. Nutrients included total phosphorus (TP) and soluble reactive phosphorus (SRP). For this study, values with salmon were taken from the downstream reach after salmon introduction in the fall and those without salmon were taken from the upstream reach before and after introductions; NA = not available.

Study	Location	Number of spawning adults	TP (μg/L)		SRP (μg/L)	
			With salmon	Without salmon	With salmon	Without salmon
Schuldt and Hershey (1995)	Lake Superior–McCarthy Creek	0.024/m^2	11.3	8.8	9.5	6.7
Sarica et al. (2004)	Lake Ontario	<0.1–0.25/m^2	16–40	NA	NA	NA
Rand et al. (1992)	Lake Ontario	NA	10–120	5–45	NA	NA
Johnston et al. (2004)	British Columbia	0.8/m^2	5–80	5–10	2–40	<1–2
Chaloner et al. (2004)	Alaska	0.08–0.12/m^2	NA	NA	2.4–7.5	2
This study	Natural	0.08/m^2 (Chinook salmon), 0.01/m^2 (steelhead)	15.6–15.8	16.1–20.8	1.3–1.5	0.36–1.5
This study	Manipulated	0.04–0.05/m^2	11.2–22.8	10.8–25.8	3.0–4.1	3.0–4.9

nutrients that were primarily accumulated at sea or in lakes to streams via egg deposition, carcass decomposition, and, in the case of iteroparous species, excretion.

The information about nutrient and energy transport by fish in streams derives largely from work on salmonids in the Pacific Northwest and Alaska (Gende et al. 2004; Johnston et al. 2004), which are regions with nutrient-poor waters. Spawning salmonids can have both positive and negative effects on stream ecosystems. Compared with streams without salmon runs, streams with spawning runs often have higher nutrient levels (Johnston et al. 2004; Cleason et al. 2006), which often generate higher levels of primary productivity (Richey et al. 1975; Kline et al. 1990). Johnston et al. (2004) and Wipfli et al. (1999) showed an increase in chlorophyll *a* and periphyton levels in rivers with spawning salmonids for up to several months after spawning runs. Increased production of lower trophic levels concurrent with spawning events can lead to increases in abundance and biomass for some invertebrate groups (Wipfli et al. 1998; Lessard and Merritt 2006), which may in turn provide more food for growing salmon in streams (Bilby et al. 1998; Wipfli et al. 2003), resulting in higher densities and growth of these fish.

Spawning salmon also can negatively affect stream ecosystems during their spawning runs. The construction of redds disturbs invertebrates (Hildebrand 1971; Janetski et al. 2009) and nutrients trapped in sediments thereby releasing them to the water column. This disruption can negatively affect stream communities in the long term owing to a loss of a valuable invertebrate biomass pool. Algal biomass also can decline as a result of redd construction (Moore et al. 2004). Further, evidence for positive effects of salmonid spawning runs on resident fish growth and survival is variable (e.g., Wipfli et al. 2003; Moore et al. 2004; Lang et al. 2006; Janetski et al. 2009).

The effects of introduced runs of salmon are less clear in tributaries of the Laurentian Great Lakes, which vary widely in background nutrient concentrations (a comparison of nutrient concentrations across the Great Lakes, the U.S. Pacific Northwest, and British Columbia is shown in Table 1). In nutrient-poor tributaries of Lake Superior, spawning salmon may significantly enhance water column nutrient levels, nutrient input into the invertebrate community (Schuldt and Hershey 1995), and decomposition rates of wood (Fisher Wold and Hershey 1999). Results for more nutrient-rich streams, however, are quite variable. Spawning Chinook salmon *Oncorhynchus tshawytscha* was not an important component of the total phosphorus budget (although on a daily basis, decomposing salmon could significantly increase phosphorus) in Lake Ontario tributaries, and chlorophyll biomass and gross primary productivity did not increase with salmon spawning (Rand et al. 1992). However, levels of mercury and nutrients increased after salmon runs in another Lake Ontario tributary (Sarica et al. 2004).

In addition to introduced runs of Pacific salmon, tributaries of the Great Lakes also experience extensive spawning runs of native fish, including walleye *Sander vitreus* and various species of suckers (Catostomidae). Unlike most introduced Pacific salmonids, native fish in the Great Lakes are often iteroparous with low mortality rates during spawning runs. Furthermore, these species are broadcast spawners and do not disturb sediments during spawning. The effect of these native fish on stream communities in the Great Lakes has not been thoroughly studied. However, several recent studies on the effect of spawning catostomids in oligotrophic streams in Michigan have revealed variable effects of these species on stream communities. During catostomid spawning runs in Lake Michigan tributaries, dissolved phosphorus concentrations (Flecker et al. 2010) and soluble reactive phosphorus, ammonia, and the growth rates of algae and caddisfly larvae increased (Childress 2010). However, spawning catostomids did not affect stream metabolism in Michigan streams (Burtner 2009).

The objectives of this study were to determine the relative effects of adfluvial fish on the ecology of Great Lakes streams under natural and mimicked spawning conditions. Specifically, we determined the effects of spawning Chinook salmon and steelhead *O. mykiss* (anadromous rainbow trout) on stream nutrient levels, invertebrate biomass and abundance, and resident fish density, stomach contents, and growth in two tributaries to the Muskegon River, a large Lake Michigan tributary in the lower peninsula of Michigan. We hypothesized that semelparous Chinook salmon would have more of an effect on nutrient levels and invertebrate density and biomass than iteroparous steelhead owing to the mortality and decomposition of salmon carcasses after spawning. We further hypothesized that egg consumption by resident fish would be high in both fall and spring and would increase the rate of fish growth compared with growth in control sites without salmonid egg introductions.

METHODS

To consider the ecological impacts of adfluvial fish on stream trophic levels, we used a before–after design, controlling for natural variation in stream environments with a control–treatment reach pairing (Cleason et al. 2006). We sampled two tributaries of the Muskegon River, a tributary of Lake Michigan, before and after spawning events. To control for natural fluctuations in ecological response variables, we sampled both streams upstream and downstream from spawning fish or carcass introductions. Bigelow Creek (henceforth the "natural stream"), a tributary of the Muskegon River, is open to adfluvial spawning fish and provided a natural setting for determining the effect of adfluvial fish on stream communities. The Middle Branch River (henceforth the "manipulated stream"), a tributary of the Muskegon River located above a migration barrier, provided a controlled setting where known numbers of carcasses and eggs of adfluvial species could be added. Habitat characteristics of both streams were similar in width, flow, velocity, discharge, and substrate composition (Table 2).

We established two 100-m-long sampling reaches, one upstream and the other downstream from spawning areas, or carcass or egg introductions, each separated by a minimum distance of 200 m in both the manipulated and natural streams. In the manipulated stream, only the downstream reach (hereafter referred to as treatment) received egg- and carcass-addition treatments while the upstream reach served as a control (hereafter referred to as control). In the natural stream, the downstream reach (hereafter referred to as the spawn) maintains high densities of spawning Chinook salmon and steelhead while the upstream reach (hereafter referred to as reference) was not generally used for spawning by either species. While the reference reach was accessible to spawning Chinook salmon and steelhead in all but one season of the study (fall 2005) owing to the destruction of a beaver dam between the two reaches during the winter of 2005–2006, we only captured two spawning salmonids there during the course of our study. We therefore decided that this reach was reflective of background ecosystem processes in the natural stream.

We added carcasses and eggs to the manipulated stream in both spring and fall to approximate previously observed densities of spawning Chinook salmon (800 adults/ha) and steelhead (100 adults/ha) in Bigelow Creek (Carl 1980; Swank 2005) and in the nearby Pere Marquette River (Workman 2002). In fall of 2005 (October 8) and 2006 (October 23), we staked (Chaloner et al. 2002a) 47 (0.168 kg/m^2) and 36 (0.165 kg/m^2) Chinook salmon carcasses, respectively, from the Little Manistee Weir in Manistee, Michigan, into the streambed of the upper 60 m of the treatment reach. Carcasses were placed in six groups separated by 10 m, each group consisting of approximately six to eight individuals. In spring of 2006 (April 13, May 6, May 14) and 2007 (April 29, May 20), eggs from two to four females (for a total of 6–8 females per season) were placed into open egg chambers at five locations throughout the upper 60 m of the treatment reach to mimic spillage out of redds during spawning. To determine the effect of spawning adfluvial salmonids under natural conditions, we sampled the natural stream before and during salmonid spawning runs during fall 2005 and 2006 and spring 2006 and 2007. We attempted to sample the natural stream at the height of spawning and after spawning, but owing to the protracted spawning of both Chinook salmon and steelhead, this was often not possible.

Nutrients.—Within each reach, we collected one to three water samples from at least three (upstream, midstream, and downstream) sites to determine water column nutrient concentrations at time periods before and after spawning. We rinsed water bottles several times before filling with stream water and kept them on ice in the dark until samples could be processed in the laboratory. We processed all samples within several hours of collection.

We determined all nutrient concentrations on a Technicon Autoanalyzer II according to automated colorimetric procedures (APHA 2005) following details described in Davis and Simmons (1979). We analyzed total phosphorus (TP) concentrations by digesting 50 mL of unfiltered water with potassium persulfate in an autoclave. We determined soluble reactive phosphorus (SRP), nitrate-nitrogen (NO$_3$-N), and ammonia nitrogen (NH$_4^+$-N) concentrations on water samples filtered through a 0.2-μm nylon filter and stored frozen until analysis. We analyzed both SRP and TP using the molybdate–ascorbic

TABLE 2. Habitat characteristics of study sites in Bigelow Creek (a natural stream) and the Middle Branch River (a manipulated stream), both of which are tributaries to the Muskegon River. The values in parentheses are ranges.

Habitat variable	Bigelow Creek	Middle Branch
Average discharge (m^3/s)	0.9 (0.3–1.6)	1.1 (0.5–2.5)
Average velocity (m/s)	0.5 (0.2–1.3)	0.6 (0.2–2.3)
Average stream width (m)	7.2 (2.4–10.3)	9.5 (2.7–13.2)
Sediment composition	45% sand, 18.7% gravel	29.4% sand, 23.53% gravel

acid method while we determined NO_3-N and NH_3-N using the cadmium reduction and phenate methods, respectively. The laboratory method of detection limits were established at 0.5 µg P/L for SRP, 1 µg P/L for TP, 5 µg N/L for $NH_4{}^+$-N, and 0.01 mg N/L for NO_3-N.

Macroinvertebrates.—We collected one macroinvertebrate sample from each of three sites (upstream, midstream, and downstream) within each reach before and after spawning using a 0.67-m^2 Hess sampler. All invertebrates were preserved in ethanol for later identification in the laboratory. Macroinvertebrates were identified to family or genus by using keys provided by Merritt and Cummins (1996), and lengths were measured on most specimens by means of a microscope micrometer, although subsamples were sometimes taken for taxa that had more than 30 individuals. Dry weights were calculated from known weight–length regressions from Smock (1980) and Benke et al. (1999). Total invertebrate density and total invertebrate biomass were analyzed for each site.

Fish.—We estimated density, stomach content, and growth rate of fish in all reaches. We reported density trends of mottled sculpin *Cottus bairdii* and brown trout *Salmo trutta* as these were the most common species in all four reaches. We estimated fish density using a two-pass depletion approach with a barge electrofisher. Individual fish were identified to species and measured for length and weight. Stomach contents of all brown trout greater than 10 cm were sampled by gastric lavage. All stomach contents were preserved in ethanol and identified in the laboratory. Macroinvertebrates in stomachs were identified to family while other stomach content items were identified and weighed (wet weight). To place all stomach content items in similar units, macroinvertebrates were converted from dry weight to wet weight by using taxa-specific, dry weight–wet weight relationships (Hanson et al. 1997; Ciancio et al. 2007). Energy content of stomach samples was estimated based on known energy densities for salmonid eggs (9,250 J/g; Gende et al. 2004) and macroinvertebrates (range, 2,000–6,000 J/g; Hanson et al. 1997; Dieterman et al. 2004).

In fall 2006 through spring 2007, we embedded passive integrated transponder (PIT) tags into brown trout greater than 12 cm to determine growth rates and movements of individual fish between treatment–spawning and control–reference reaches. During each subsequent electrofishing event, we checked individual trout for the presence of a PIT tag. Tagged fish were identified, reweighed, and measured before release, while untagged fish were tagged. To estimate instantaneous growth rates of individual fish, we divided changes in $\log_e$-transformed length or weight by the number of days between recapture events (Isely and Grabowski 2007).

Statistical analyses.—To determine the effect of spawning Chinook salmon and steelhead on stream ecosystems, we analyzed nutrient concentrations, total invertebrate biomass (milligrams dry weight per Hess sample) and total invertebrate abundance (number per Hess sample) using either an analysis of variance (ANOVA) or a Kruskal–Wallis test (depending on whether normality assumptions of ANOVA were met)

separately for each stream and each season. To control for natural changes in these metrics over time, nutrient and invertebrate metrics were calculated as

$$D_{ikl} = \log_e(RC_{ikl}) - \log_e(ST_{ikl}),$$

where D is difference between the reference–control reach and the treatment–spawn reach, RC is the mean value of three sites for either the nutrient concentration or invertebrate metric at the reference or control reach, ST is the value of either the nutrient concentration or invertebrate metric at the spawn or treatment reach, i is the season, k is the stream, l is the site (upstream, midstream, and downstream) in the spawn or treatment reach (Cleason et al. 2006). An ANOVA or a Kruskal–Wallis analysis was then performed over time to determine whether any metrics increased postspawning (Cleason et al. 2006). Posthoc tests from significant ANOVAs were performed with a Tukey's test (no significant Kruskal–Wallis tests were observed after Bonferroni correction). All analyses were conducted in SPSS version 18.0 (PASW Statistics 2010) and were considered significant at $\alpha = 0.05$ after adjusting for multiple comparisons with Bonferroni correction (Zar 1999).

To determine the effect of spawning Chinook salmon and steelhead on the diet of resident trout, we performed two separate analyses. First, we determined whether individual resident trout benefited from spawning activities by comparing energy in diets of individuals with and without eggs in their stomachs at the time of sampling. Second, we compared the effect of spawning fish on the entire brown trout population within a reach by comparing the energetic composition of resident fish diet in the control (or reference) reach to the treatment (or spawn) reach after egg introduction. Comparisons were conducted for each stream and season with a Mann–Whitney U-test owing to violations of normality assumptions within groups. Because of low sample sizes, no diet comparisons were made in the natural stream in the spring. Differences were considered significant at the $\alpha = 0.05$ level and adjusted for multiple comparisons with the Bonferroni corrections. We compared differences in growth rates of PIT-tagged individual fish between upstream and downstream reaches using a t-test ($\alpha = 0.05$). Growth rate estimates were based on daily growth rates for the entire sampling time period (2006–2007). All analyses were conducted in SPSS version 18.0 (PASW Statistics 2010).

RESULTS

Natural Stream

The effects of salmonid spawning on the ecology of the natural stream varied by season and year, but in general were minimal, especially on nutrient and invertebrate metrics. No significant changes were observed in nutrient concentrations or invertebrate counts or biomass in the spawning site compared with the reference site (Figures 1 and 2).

Fish species densities had a variable response to salmonid spawning or carcass introductions. In the natural stream,
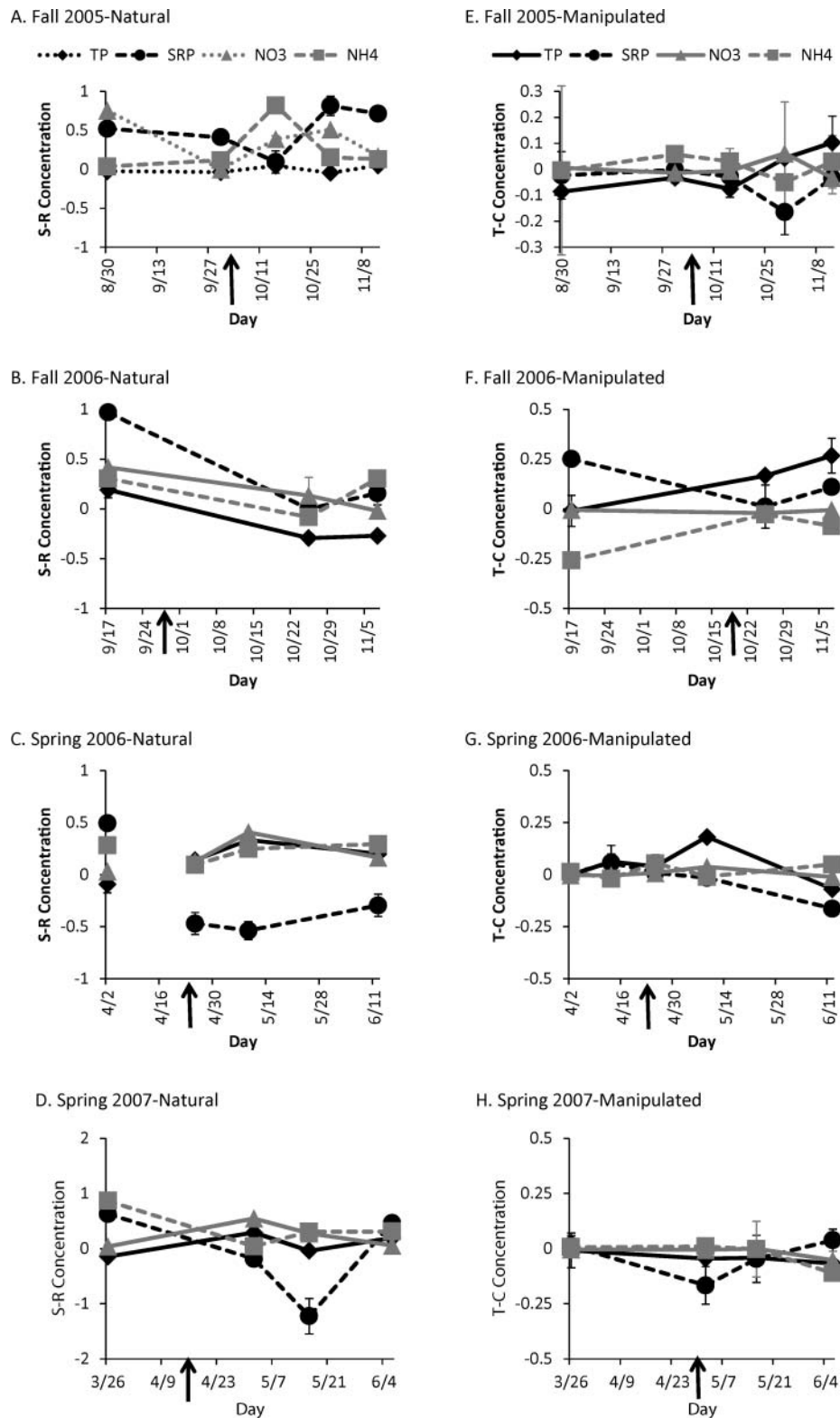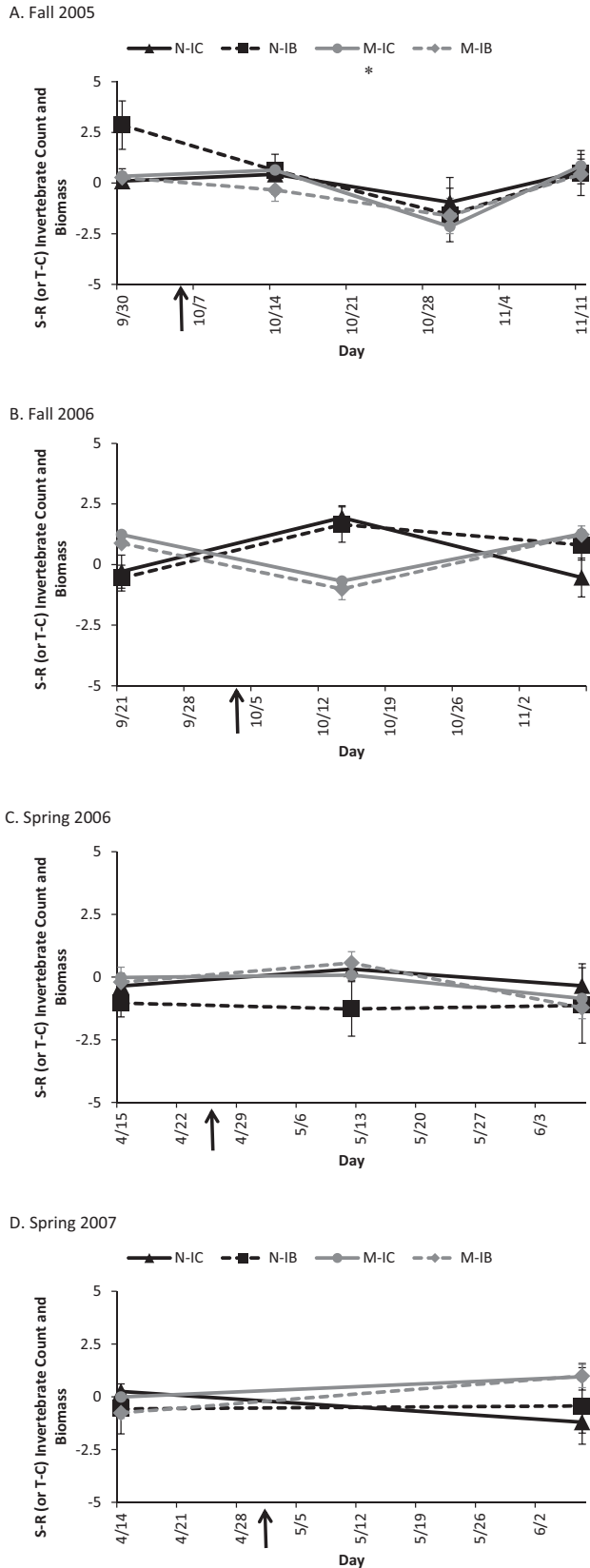
FIGURE 1.   Mean (± SE) difference between treatment (or spawning) and control (or reference) in nutrient concentrations for the natural stream in (**A**) fall 2005, (**B**) fall 2006, (**C**) Spring 2006, and (**D**) Spring 2007, and in the manipulated stream in (**E**) fall 2005, (**F**) fall 2006, (**G**) spring 2006, and (**H**) spring 2007. Nutrient concentrations include total phosphorus (TP, µg/L), soluble reactive phosphorus (SRP, µg/L), ammonia nitrogen (NH_4^+-N, mg/L), and nitrate (NO_3-N, mg/L). In the natural stream, arrows on *x*-axis in fall represent the time when adult fish were first observed while arrows in spring represent the last sampling time when adult fish were observed. In the manipulated stream, carcasses were introduced in fall after September and eggs were introduced in spring after April (noted by arrow). Note the negative *x*-axis.

FIGURE 2. Mean ($\pm$ SE) difference between treatment (or spawning) and control (or reference) of invertebrate counts (IC, solid line) and biomass (IB, dashed lines) for the natural stream (N, black) and the manipulated stream (M, gray lines) in (**A**) fall 2005, (**B**) fall 2006, (**C**) spring 2006, and (**D**) spring 2007. In the natural stream, arrows in fall represent when adult fish were first observed while arrows in spring represent the last sampling time when adult fish were observed. In the manipulated stream, carcasses were introduced in fall after September and eggs were introduced in spring after April (noted by arrow). An asterisk ($*$) denotes significant differences (ANOVA, $P < 0.006$, Bonferroni corrected). A significant difference occurred between October 28, 2005, and the remainder of the sampling dates (Tukey's test, $P < 0.006$ for all comparisons). Note the negative x-axis.

densities of mottled sculpin were always greater in the reference reach than in the spawn reach (Figure 3). In fall 2005, the density of mottled sculpin declined during peak spawning in the spawn reach relative to the reference reach. The same phenomenon was observed in May of 2006 (Figure 3A, C). Densities of brown trout increased in the downstream reach during peak spawning in fall 2005 (mid-October; Figure 1A) and fall 2006 (early November; Figure 3A, B). In the spring, brown trout densities did not vary directly with steelhead spawning; instead, they peaked in June after steelhead spawning was completed by May (Figure 3C, D).

Eggs were an important energy source for resident trout in the spawn reach. The proportion of fish that consumed eggs varied depending on the sampling date. In 2005, 55% of the individuals consumed eggs during peak spawning (46% overall). In 2006, the number of individual trout that consumed eggs was even higher during peak spawning (73–77%) and was high overall (75%). Eggs also comprised a high percentage by weight of the diet of trout residing in the spawn reach (44–91%; Figure 4A, B). Based on stomach content analysis, fish that consumed eggs also consumed more energy compared with those that did not consume eggs in fall 2005 ($U = 43$, $Z = -5.554$, $n = 75$, $P < 0.001$) and fall 2006 ($U = 15$, $Z = -6.751$, $n = 65$, $P < 0.001$; Figure 5A). However, brown trout residing in the spawn reach (those consuming eggs as well as those that did not) did not have a significantly higher mean energy intake (as evidenced by stomach content analysis) than fish residing in the reference reach in fall 2005 ($P > 0.0063$ after Bonferonni correction; Figure 5B) and fall 2006 ($P > 0.05$; Figure 5B).

The number of recaptured fish was low in the natural stream (48 tagged fish, of which 20% were recaptured), but no fish were recaptured in a different reach from which they were tagged. Despite the large energy content in trout stomachs in the spawn reach, we did not observe any difference between reaches in growth rates of tagged fish ($P > 0.15$; Figure 6A, B).

Manipulated Stream

The effects of carcass introductions on the ecology of the manipulated stream also varied by season and year, but in general were minimal, especially on nutrient and invertebrate densities. There were no significant effects on nutrient concentrations
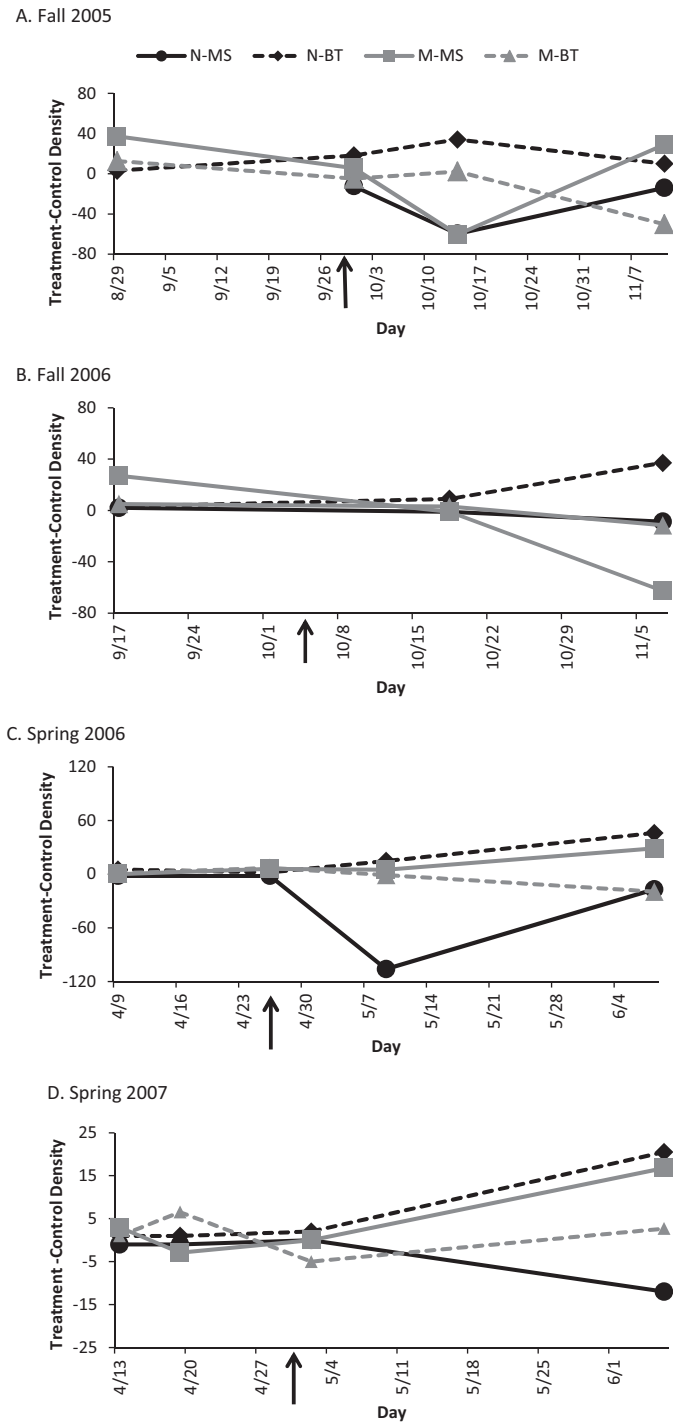
FIGURE 3. Difference between treatment (or spawning) and control (or reference) densities of mottled sculpin (MS, solid lines) and brown trout (BT, dashed lines) in the natural stream (N, black) and manipulated stream (M, gray) in (**A**) fall 2005, (**B**) fall 2006, (**C**) spring 2006, and (**D**) spring 2007. In the natural stream, arrows in fall represent when adult fish were first observed while arrows in spring represent the last sampling time when adult fish were observed. In the manipulated stream, carcasses were introduced in fall after September and eggs were introduced in spring after April (denoted by arrow). Note the negative x-axis.

(Figure 1). However, in fall 2005 there was a significant decline in invertebrate density ($F_{3,8} = 16.021$, $P = 0.001$; Figure 2A) on the second postmanipulation sampling date.

Mottled sculpin and brown trout densities varied across and within seasons (Figure 3). In the fall, neither brown trout nor mottled sculpin density increased in the treatment reach after carcass and egg introductions (Figure 3A, B). In spring, mottled sculpin numbers did increase in the treatment reach relative to the control reach, while brown trout densities did not change (Figure 3C, D).

As was the case in the natural stream, eggs were an important energy source for resident trout in the treatment reach. The proportion of fish that consumed eggs varied depending on the sampling date. Peak proportions of fish that consumed eggs were 93, 87, 23, and 87% for fall 2005, fall 2006, spring 2006, and spring 2007, respectively. The overall frequency of salmonid eggs in trout diets was similar (63–67%) for all seasons except spring 2006 (8%). Salmonid eggs also comprised a high percentage of the diet by weight (Figure 4E, H). Fish that consumed eggs had a higher mean energy intake (based on stomach contents) than fish that had no eggs in their diets in fall 2005 ($U = 99$, $Z = -7.324$, $n = 118$, $P < 0.001$), fall 06 ($U = 46$, $Z = -6.592$, $n = 78$, $P < 0.001$), and spring 2007 ($U = 25$, $Z = -6.63$, $n = 87$, $P < 0.001$; Figure 5C). Finally, the overall mean energy of stomach contents of all brown trout (both those that consumed eggs as well as those that did not) residing in the treatment reach was higher than that of those residing in the control reach in all seasons except spring 2006 (fall 2005: $U = 137$, $Z = -3.949$, $n = 59$, $P < 0.001$; fall 2006: $U = 204$, $Z = -2.936$, $n = 55$, $P = 0.003$; spring 2007: $U = 202$, $Z = -2.924$, $n = 55$, $P = 0.003$; Figure 5D).

The total number of recaptured fish was higher in the manipulated stream than in the natural stream, but still represented only 24% of the numbers tagged (87 individuals tagged in total). No tagged fish were recaptured in a reach other than where they were tagged. As was the case in the natural stream, we observed no differences in growth rate of PIT-tagged resident trout ($P > 0.15$; Figure 6A, B) between control and treatment reaches during the course of this study.

DISCUSSION

We found that the effects of spawning salmonids on the ecology of streams in the Great Lakes area were variable depending on year and season. Surprisingly, effects on nutrient chemistry and macroinvertebrates were not greater in fall than in spring, which was what had been expected. Furthermore, there was no difference between the natural and the manipulated stream with regards to effects of spawning activity on macroinvertebrates or nutrients. Energy consumption of resident fish increased in both fall and spring in the manipulated stream after carcass introduction. Our results show that the most likely effect of spawning Chinook salmon and steelhead on our study streams was through the consumption of their eggs by resident trout. More research
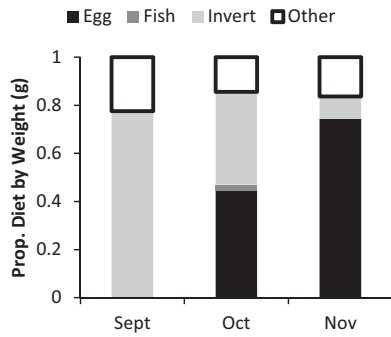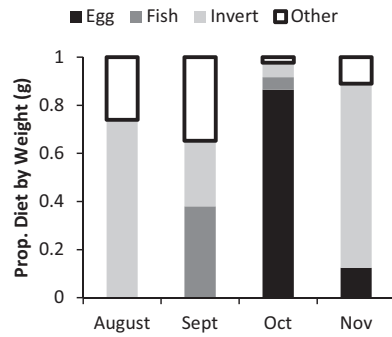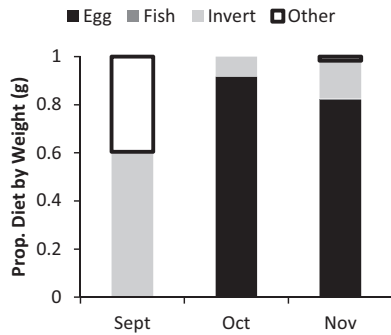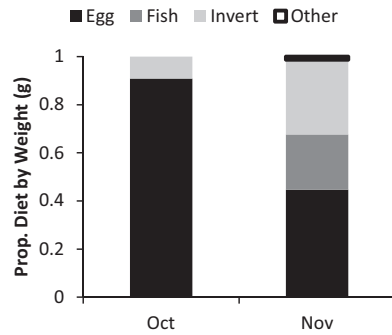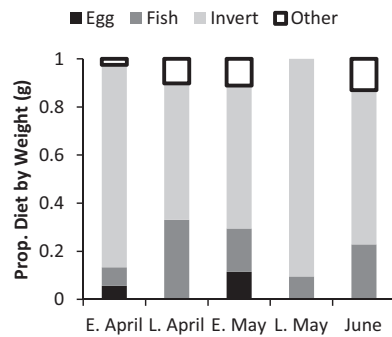
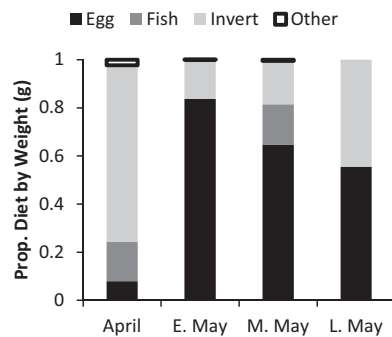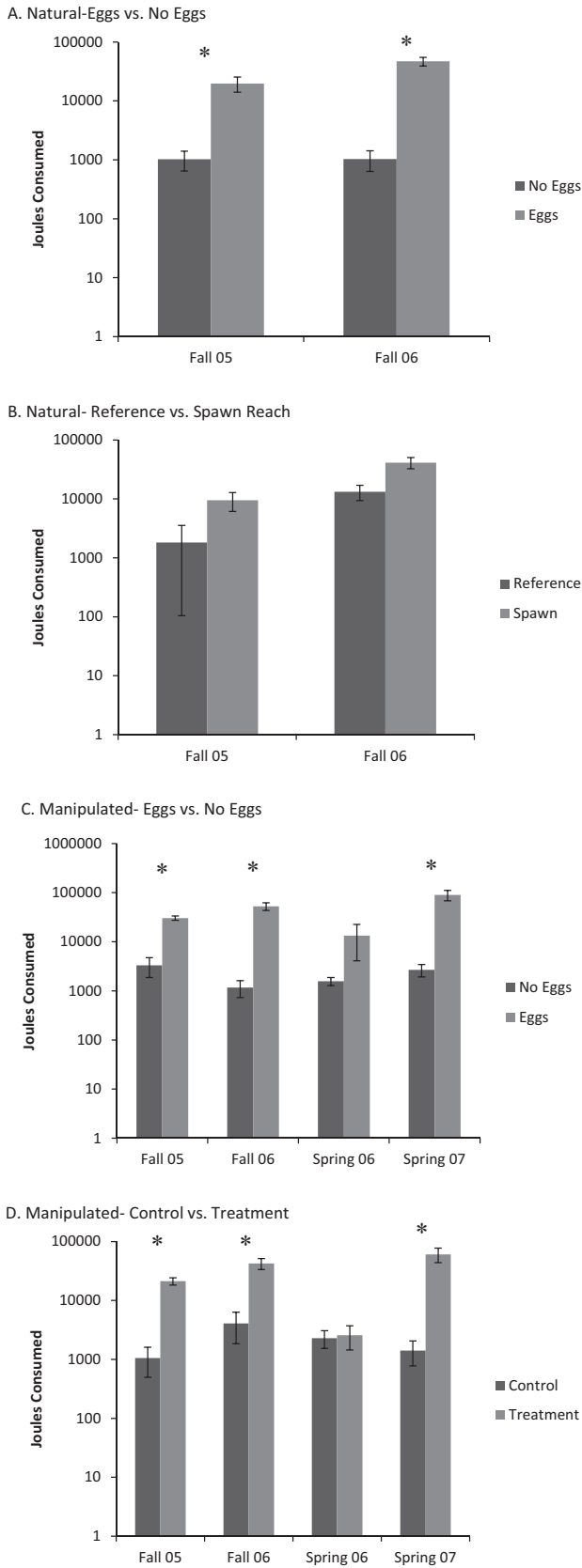FIGURE 4. Mean diet proportions by weight (g) of adult brown trout sampled from the spawning reach in the natural stream in (**A**) fall 2005, (**B**) fall 2006, (**C**) spring 2006 (none available), and (**D**) spring 2007 (none available), and in the treatment reach in the manipulated stream in (**E**) fall 2005, (**F**) fall 2006, (**G**) spring 2006, and (**H**) spring 2007. Mean proportions were only calculated if more than three individuals were sampled within a reach. In the manipulated stream, carcasses were introduced in fall after September and eggs were introduced in spring after April (denoted by arrow).

A. Natural-Eggs vs. No Eggs

B. Natural- Reference vs. Spawn Reach

C. Manipulated- Eggs vs. No Eggs

D. Manipulated- Control vs. Treatment

is needed to determine whether egg consumption leads to increased growth and survival of other resident fish species.

We hypothesized that spring fish would not affect water chemistry as much as would fall fish because spring fish survive spawning while fall fish die and leave behind carcasses that decompose within streams. However, we did not observe significant changes in stream nutrients in either the manipulated or natural stream, and the overall patterns in nutrient concentrations were highly variable. Other studies in the Great Lakes also found variable effects of spawning fish on nutrient concentrations (Rand et al. 1992; Schuldt and Hershey 1995). Our results showed there were minimal effects of spawning salmon on background nutrient levels and they are consistent with the results found by Rand et al. (1992) in a tributary of Lake Ontario but differ from those of Schuldt and Hershey (1995) in a tributary of Lake Superior. Runs of native catostomids in oligotrophic streams resulted in increased SRP and NH_4^+-N during spawning of these iteroparous fish (Childress 2010; Flecker et al. 2010). The variable results we observed compared with these other Great Lakes studies could have resulted from the presence of higher background nutrients, lower carcass densities, or lower discharge in our study streams. A comparison of background nutrient concentrations among streams in the Great Lakes region and the Pacific Northwest (Table 1) revealed that some streams in the Great Lakes area have background TP and SRP concentrations similar to streams in the Pacific Northwest. However, when comparing nutrient levels without the effect of adfluvial fish, streams in the Great Lakes region are more variable and have higher maximum concentrations of nutrients than do streams in the Pacific Northwest. Although streams in the Great Lakes region tend to have lower densities of spawning salmon, the salmon densities in the natural stream in our study were similar to densities in two of the three streams sampled by Chaloner et al. (2004), which experienced increases in background nutrient levels in reaches with salmon. Stream discharge also was lower in both our study streams than in those studied by Chaloner et al. (2004), so loss of nutrients downstream is unlikely. The relative influence of background nutrient concentrations, discharge, or carcass densities when considered alone cannot explain stream responses to nutrient additions via spawning salmon. Rather, it is likely that all three play a role in determining the potential for bottom-up effects of adfluvial fish on stream ecosystems.

FIGURE 5. Mean ($\pm$ SE) energy consumption as number of joules (J) consumed by adult brown trout in fall 2005 and 2006 and spring 2006 and 2007 in the natural stream for (**A**) fish with eggs in their stomachs and those without and (**B**) in reference and spawn reaches during spawning, and in the manipulated stream for (**C**) fish with eggs in their stomachs and those without and (**D**) in the reference and spawn reaches during spawning. Significant differences are noted with an asterisk (*) between energy consumed by fish with and without eggs in their stomachs for each season. Significant differences are noted with an asterisk (*) between energy consumed by fish in the reference and spawn reaches (or in the control and treatment reaches) for each season. Note the logarithmic scale on all axes.
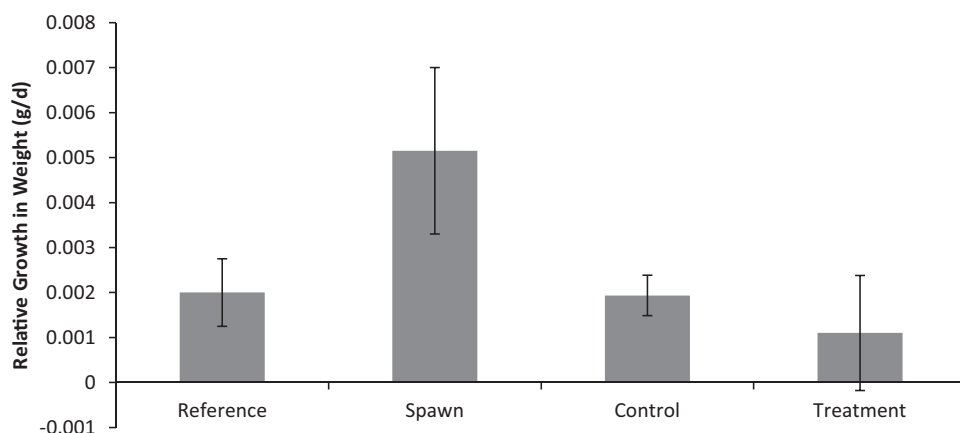
A. Length
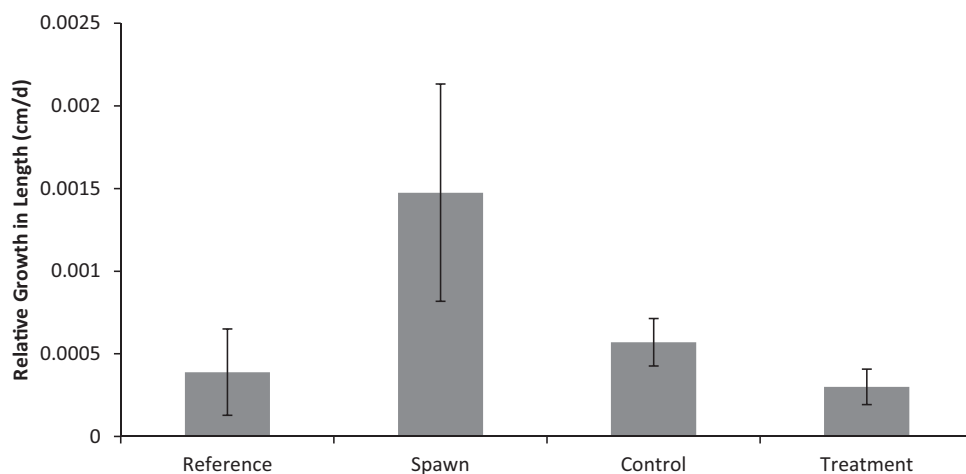
B. Weight

FIGURE 6. Mean ($\pm$ SE) instantaneous growth in (**A**) length (cm/d) or (**B**) weight (g/d) of adult PIT-tagged trout over time in response to Chinook salmon and steelhead spawning in Bigelow Creek (reference sites lacked adult fish while the spawn reach did not) or carcass or egg introductions in the Middle Branch River (control sites did not receive introductions while treatment sites did). No significant differences were observed when comparing reference and spawn reaches or when comparing control and treatment reaches.

In the Pacific Northwest, the effect of spawning salmon on nutrient concentrations between streams with natural runs of spawning salmon and streams with carcass additions differed. Janetski et al. (2009) found that increases in nutrient levels were 5–10 times higher in streams with natural runs of Pacific salmon than in streams that used carcass additions, a result not supported by our study. However in our study, background concentrations of nutrients tended to be greater in the manipulated stream (Table 1), which could make enhancement of nutrients due to carcass additions more difficult to observe than in the natural stream. Furthermore, the overall density of carcasses we added to the manipulated stream was slightly lower (especially in 2006) than the carcass density in the natural stream, or than densities reported from the Pacific Northwest (Chaloner et al. 2004; Johnston et al. 2004). Janetski et al. (2009) found no effect of spawning salmon on nutrients and invertebrates at low

biomass levels (0.1–1 kg/m^2). The amount of salmon tissue we added to the manipulated stream was 0.165–0.168 kg/m^2, well within that range. Therefore, observed spawning densities of Chinook salmon and steelhead found in many tributaries of the Great Lakes may not be great enough to increase nutrient concentrations significantly above the background nutrient concentrations.

We also hypothesized that Chinook salmon would positively affect macroinvertebrate biomass and abundance owing to increased productivity and food availability due to the presence of carcasses. As was the case for water chemistry, we found no statistical evidence to support this hypothesis in either the natural stream or the manipulated stream. The effect of spawning salmon on invertebrate communities often depends on which taxonomic group is being studied (Chaloner et al. 2002b; Lessard and Merritt 2006) and whether redds are being

constructed in the areas studied. Since redd construction can dislodge invertebrates (Field-Dodgson 1987), spawning salmon can actually result in declines of invertebrates. For example, Moore and Schindler (2008) found a 75–85% decrease in insect biomass in streams with spawning densities of 0.1 salmon/m^2. Sediment type may also play a role in the response of macroinvertebrates to salmon spawning. Benthic macroinvertebrates associated with larger sediment sizes (>32 mm) tend to have a positive response to spawning events (Janetski et al. 2009). Both the natural stream and the manipulated stream in our study contained a variety of sediment sizes, of which at least 25% of the substrate was sand in both rivers. As such, one might not expect to observe positive effects of adfluvial fish on benthic invertebrates in our study systems as, on average, some areas would show positive effects and some negative. Studies that use carcass manipulation rather than observations of naturally spawning fish may be more likely to observe positive effects on invertebrate communities because sediments are not disturbed by spawning fish (Janetski et al. 2009). Our study, however, found no evidence that manipulated streams have more positive effects on macroinvertebrates compared with streams that have natural runs. Nonetheless, studies in the Great Lakes region have observed positive effects on benthic invertebrates owing to the presence of adfluvial fish (e.g., Schuldt and Hershey 1995; Childress 2010), and as such, the importance of this link should not be dismissed. Future studies should therefore control for the potential of positive and negative effects of spawning activity when addressing the role these fish play in stream ecosystems.

It is possible that we were unable to detect changes in density and biomass of invertebrates owing to low sample size. Previous work has suggested use of at least three replicate benthic samples (Resh and McElravy 1993). Chiasson (2009) found that small sample sizes resulted in large confidence intervals, which decreased the ability to detect differences among sites. Furthermore, Chiasson (2009) found that the number of samples required to decrease the coefficient of variation by at least 10% ranged from three to six in New Brunswick streams. As such, a lack of significant effects of salmon introductions on invertebrates in our study streams may be due to low power owing to small sample sizes.

The response of resident trout and mottled sculpin to salmonid introductions also varied between streams and seasons. Mottled sculpin density did not increase in response to spawning salmon in either stream despite previous work that showed mottled sculpin consume salmon eggs (Merna 1979). However, resident trout density did increase in the spawning reach during peak spawning in the natural stream in fall of 2005 and 2006. Others have also noted increases in fish density that are coincident with spawning events. Bilby et al. (1998) found density of age-0 coho salmon *O. kisutch* and steelhead increased during spawning runs, then slowly decreased after spawning. Spawning activity probably attracts individuals living outside spawning reaches, perhaps in response to increased food resources. Surprisingly, we did not observe differences in densities of brown trout in spring until after peak spawning. Lower spring spawning density, high flow rates, and increased abundance of food resources associated with spring may reduce the importance of spawning steelhead on stream residents in Great Lakes tributaries.

Spawning anadromous and adfluvial fish may increase energy intake of resident fish in both the Pacific Northwest and the Great Lakes region by providing calorically rich eggs. In a study of rainbow trout consumption during spawning of sockeye salmon *O. nerka*, Scheuerell et al. (2007) found energy intake increased by 480–620%, and the bulk of this increase came from salmon eggs, salmon flesh, and blow flies. In the natural stream, trout that ate eggs benefited by increased energy content in the gut, but we did not see increased energy consumption in the spawn reach relative to the reference reach in either fall 2005 or fall 2006. In the manipulated stream in fall 2005, fall 2006, and spring 2007, we observed increases in the average amount of energy consumed by resident trout that consumed eggs compared with those that did not consume eggs, as well as increases in the overall energy consumption of all trout residing in the treatment reach after the addition of eggs. The lack of response by fish in the manipulated stream in spring 2006 was probably due to the sampling design and a high stream flow that occurred after the placement of two sets of eggs, which quickly dislodged eggs from their containers on the streambed. Despite this, our study clearly demonstrates that eggs from both Chinook salmon and steelhead are an important diet item for resident brown trout.

Increases in energy consumption can increase resident fish growth (e.g., Bilby et al. 1998; Wipfli et al. 2003) and survival, but may also be a pathway by which contaminants are transmitted (Merna 1979). While variable, the proportion of fish with eggs in their stomachs during spawning was high (46–75%), which suggests that many fish use this source of energy, and the high proportion by weight of eggs in the diets suggests that this resource is very valuable to stream residents.

The increased energy intake from salmon eggs for resident fish did not influence fish growth in length or weight in our study, as has been observed in other studies of Pacific salmon (e.g., Bilby et al. 1998; Wipfli et al. 2003). Unfortunately, owing to the low recapture rate, it was not possible to determine whether individuals that consumed eggs had greater increases in length or weight relative to those recaptured fish that did not consume eggs. Lang et al. (2006) found no survival advantage for outmigrating juvenile coho salmon in an Alaskan stream due to the presence of fall spawning adult coho salmon, although the growth and condition of juveniles did increase in areas with spawning activity. The length of time that eggs are available, as well as the number of eggs available, probably determines the effect that eggs have on stream ecosystems and warrants further study.

In addition to spawning Pacific salmon and steelhead, tributaries of the Great Lakes have other adfluvial fishes, including walleye and suckers, which may also contribute energy to the streams in which they spawn. Historically, tributaries of

the Great Lakes supported large spring spawning runs of these iteroparous broadcast spawners (Flecker et al. 2010). While their eggs are not as rich in energy or as large as those of salmonids, walleyes and suckers have higher fecundities (up to 300,000 eggs per female) and spawn over open river substrates, thereby making eggs more available to the entire stream community. Therefore, in contrast to spawning salmonids in the Pacific Northwest and Alaska, the primary mechanisms by which these adfluvial fishes in the Great Lakes may affect stream ecosystems is through egg deposition, excretion, and carcass decomposition (Childress 2010; Flecker et al. 2010). Future work in the Great Lakes is required to determine the role of these native adfluvial fishes on stream ecosystems and resident fish growth and survival in the Great Lakes.

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