

Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams

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Abstract

Spawning Pacific salmon (*Oncorhynchus* spp.) historically transported massive quantities of marine-derived nutrients (MDN) into nutrient-poor streams of the Pacific Northwest. In southeast Alaska, we measured the effects of MDN on streamwater chemistry and epilithon standing stock (1) through time during two consecutive years in one stream, Fish Creek; (2) over space in six salmon streams; and (3) in a controlled mesocosm experiment. In Fish Creek during strong salmon runs in 2000 and 2001, streamwater concentrations of ammonium (NH_4^+) increased 10-fold and soluble reactive phosphorus (SRP) increased by 4- to 7-fold in the presence of salmon. NH_4^+ and SRP also increased with distance downstream in the salmon reach, likely related to a 'carcass-loading' effect. In contrast, nitrate (NO_3^-) and dissolved organic carbon concentrations varied only with discharge. In 2000, epilithon chlorophyll *a* increased by 20-fold during the salmon run, whereas no significant change was observed in 2001. Over space, the multistream survey revealed consistent increases in NH_4^+ and SRP, but no pattern in epilithon response to the salmon run. In the mesocosm experiment, NH_4^+ , SRP, and epilithon standing stock all increased in the presence of salmon carcasses in artificial streams. Overall, salmon clearly increased the concentrations of important dissolved nutrients in southeast Alaska streams. Responses in epilithon were more variable, however, suggesting that multiple environmental factors including light and disturbance likely regulate epilithon growth in salmon streams. Nutrient mass transport estimates revealed that a substantial amount of MDN (46%–60% depending on element) is exported directly back to the estuarine environment, suggesting that salmon represent a key marine–freshwater coupling in nutrient cycling.

Terrestrial, freshwater, and marine ecosystems are connected through the transfer of nutrients and organic matter (e.g., Wallace et al. 1997; Burkart 1999). The most common pathway for nutrient and energy transfer is usually downstream from the land to fresh water and finally to the sea. However, previous research has shown that nutrients can flow against this gradient (e.g., Anderson and Polis 1999). The annual migration of Pacific salmon (*Oncorhynchus* spp.) from salt water to natal freshwater spawning grounds is an example of this reverse transfer of organic matter and nutrients. Each year in northwestern United States and Canada, over 100 million Pacific salmon return from the ocean to fresh water to spawn and die (Gresh et al. 2000). Evidence from stable isotope analyses reveals that nutrients derived from the salmon are incorporated into terrestrial and freshwater food webs (Kline et al. 1993; Bilby et al. 1996; Chaloner et al. 2002), but the specific mechanisms by which these marine-derived nutrients (MDN) enter food webs are not fully understood.

One possible pathway for the assimilation of MDN into

freshwater food webs is by bottom-up processes involving the uptake of dissolved nutrients by algae and bacteria growing on rocks (i.e., epilithon). When live salmon or decomposing carcasses are present in streams or lakes, water column concentrations of ammonium and phosphorus can increase (Sugai and Burrell 1984; Minakawa and Gara 1999). Nutrient release from spawning salmon has also been associated with increased phytoplankton chlorophyll *a* concentrations in lakes (Mathisen 1972; Schmidt et al. 1998). In contrast, there are conflicting results as to how much salmon-derived nutrients increase epilithon abundance in streams (Schuldt and Hershey 1995; Wipfli et al. 1998; Minakawa and Gara 1999). Previous studies have rarely examined responses in both dissolved nutrients and epilithon abundance to spawning salmon (but see Schuldt and Hershey 1995; Minakawa and Gara 1999). Furthermore, no previous studies have quantified responses over multiple years in the same stream or across numerous streams to examine temporal and spatial patterns of nutrients and epilithon in salmon streams.

The goal of this study was to determine the effects of spawning salmon on dissolved nutrient concentrations and epilithon abundance in southeast Alaska streams. Specifically, we examined whether responses in nutrients and epilithon were consistent temporally (year-to-year in the same stream) and spatially (across several streams) and then estimated causes of any spatial and temporal variability. We hypothesized that spawning salmon would increase stream-dissolved nutrient concentrations, which would subsequently increase epilithon standing stock. By examining these responses in natural streams (temporally and spatially) and in artificial stream experiments, we hoped to gain a better understanding about mechanisms controlling an important resource (epilithon) in salmon streams.

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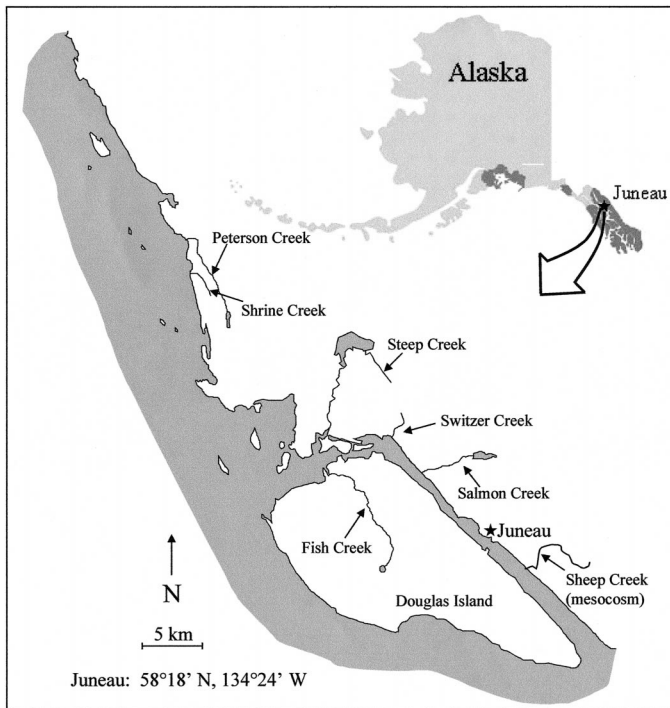


Fig. 1. Location of study streams near Juneau in southeast Alaska.

Methods

Site descriptions—Juneau, Alaska has a maritime climate with mean monthly air temperatures ranging from -2°C to 14°C and average annual precipitation of 137 cm. We studied six first–third-order salmon streams near Juneau in southeast Alaska (Fig. 1). Five species of Pacific salmon spawn in southeast Alaska: *Oncorhynchus gorbushcha* (pink salmon), *O. keta* (chum salmon), *O. kisutch* (coho salmon), *O. nerka* (sockeye salmon), and *O. tshawytscha* (chinook salmon). The species and number of spawning salmon varied among streams, but all streams had substantial salmon runs during our study (Table 1).

Study design—We examined year-to-year variation in Fish Creek, a third-order stream that had a natural fish barrier (i.e., waterfall) at approximately 4 km from the mouth of the stream, which prevented any upstream migration of spawning salmon. Surface water and benthic epilithon were sampled biweekly during July, August, and September of 2000 and 2001 upstream and downstream of the barrier. Three sites were selected within both the upstream (= upper) and downstream (= lower) reaches to use as spatial replicates for characterizing response variables in each study reach.

In 2001, we examined stream-to-stream variation in an additional five streams. The six streams (including Fish Creek) varied in size and salmon enrichment (Table 1), and all but one (Switzer Creek) had a natural fish barrier that allowed for discrete upstream–downstream comparisons. Three sites were sampled in the lower reach of each stream and one to three sites (due to accessibility) were sampled in the upper reach. Samples were collected in each stream once before the salmon run and a second time during the salmon run.

Field and laboratory methods—At each site, we collected three replicate samples for nutrient analyses and five replicate epilithon samples for Chl *a* standing stock and ash-free dry mass (AFDM) analysis. Canopy cover was estimated at each site using a spherical densiometer. Stream discharge was measured in both the upper and lower reaches using the velocity-area method (Gore 1996).

Water samples were analyzed for ammonium (NH_4^+), nitrate (NO_3^-), soluble reactive phosphorus (SRP), and dissolved organic carbon (DOC). Ammonium was measured within 4 h after sampling on a Turner TD-700 fluorometer using the fluorometric ammonium analysis technique (lower limit: $0.5 \mu\text{g L}^{-1}$, upper limit: $110 \mu\text{g L}^{-1}$) (Holmes et al. 1999). Nitrate and SRP samples were filtered in the field through a Whatman GF/F filter ($0.7 \mu\text{m}$) and then frozen until analyzed (usually within 2 weeks of sampling). Nitrate was analyzed manually using the hydrazine reduction method adapted from Kamphake et al. (1967) (lower limit: $1 \mu\text{g}$

Table 1. Characteristics of study streams near Juneau, Alaska.

	Fish Creek	Peterson Creek	Salmon Creek	Shrine Creek	Steep Creek	Switzer Creek
Location	58°19'N 134°35'W	58°29'N, 134°46'W	58°19'N, 134°28'W	58°28'N, 134°47'W	58°24'N, 134°34'W	58°21'N, 134°20'W
Mean discharge during study (L s^{-1})	3,260	1,660	1,300	33.4	323	28.2
Mean canopy coverage	55%	60%	75%	80%	50%	75%
Anadromous Pacific salmon species*	pink, chum, chinook, coho	pink chum, coho	pink, chum, coho	pink, chum, coho	sockeye, pink, chum, coho	pink, chum, coho
Maximum mass of salmon run (kg wet mass)*	122,000	223,000	110,000	NA§	8,000	3,000
Estimated spawner densities in 2001†‡ (number m^{-2})	0.04 (0–0.14)	0.07 (0–0.53)	0.27 (0–0.83)	NA	NA	NA

* Based on Bethers et al. (1995).

† Chaloner et al. (2004).

‡ Mean (range).

§ NA, not available.

L⁻¹). SRP was analyzed using the ascorbic acid method with a 10-cm pathlength spectrophotometer cell to enable detection of low concentrations (lower limit: 0.5 µg L⁻¹) (APHA 1992). DOC samples were filtered in the field, acidified with 10 µl of 12 mol L⁻¹ hydrochloric acid per 20-ml sample, and stored at 4°C until analyzed on a Shimadzu model TOC-5000A high-temperature combustion carbon analyzer.

We measured the standing stock of both Chl *a* and AFDM of epilithon. Samples were taken from rocks using a syringe sampler based on the design of Stockner and Armstrong (1971). Epilithon samples were stored in whirl-pak bags in a cooler until returned to the laboratory. Within 4 h of collection, the samples were filtered onto Gelman A/E glass fiber filters and stored in opaque film canisters at -20°C until analyzed. Chl *a* was extracted in 10 ml of 90% buffered acetone for 24 h at 4°C, and then analyzed spectrophotometrically and corrected for phaeopigments using the trichromatic method (APHA 1992). After the chlorophyll analysis, the entire sample was transferred to an aluminum weigh pan, dried at 60°C, weighed, ashed at 550°C, reweighed, and analyzed for AFDM according to Steinman and Lamberti (1996).

We also measured epilithon primary production and community respiration in closed recirculating chambers (see Lamberti et al. 1989) placed in three of the six study streams. Incubations could not be run in all streams because of logistical constraints. Gross primary production (GPP) and respiration were measured using dissolved oxygen change from light and dark incubations, respectively (Bott 1996). These measurements were used to compute GPP and net daily metabolism (NDM).

Mesocosm—The mesocosm experiment was conducted in straight once-through artificial stream channels (each 3 m long × 18 cm wide × 23 cm deep) located next to Sheep Creek in Juneau, Alaska. This mesocosm is similar to one used by Wipfli et al. (1998). Water for the mesocosm was gravity-fed from a salmon-free reach of Sheep Creek into a header tank and then released into channels via valved individual polyethylene pipes at a flow rate of 0.6 L s⁻¹ into each channel. Sheep Creek is a second-order, cool-water stream with hatchery-supported runs of pink and chum salmon into a short lower reach. A waterfall 200 m from the mouth prevents any salmon from migrating further upstream. Shade cloth (55% light reduction) was placed over the channels to simulate light conditions in typical southeast Alaska streams (~500 µmol m⁻²s⁻¹ on cloudless days). Each channel consisted of a pool-riffle-pool sequence. The upstream pool (102 cm long) contained the carcass treatment, and the riffle (66 cm long) contained 12 unglazed clay tiles that were placed on rocks for epilithon analysis.

The mesocosm experiment was designed to examine the effects of salmon carcasses on stream dissolved nutrient concentrations and epilithon abundance under replicated, controlled conditions. Three treatments, each replicated six times, were used: low carcass (LC), high carcass (HC), and a control (no carcass). Female chum salmon (*O. keta*) carcass chunks and eggs were used for the carcass treatments. The LC and HC treatments corresponded to 6.8 kg and 13.6 kg wet mass chum salmon per square meter, or approxi-

mately 1 and 2 chum carcasses per square meter, respectively. These treatments are higher than what we observed in the natural streams but within the range found in streams in southeast Alaska (Wipfli et al. 1999). The experiment was conducted 23 August–3 September 2001. After 2 and 4 weeks, carcasses were hand-macerated to emulate physical disruption of carcasses in natural streams.

Samples for dissolved nutrient concentrations and epilithon abundance were taken after 2, 4, and 6 weeks. Triplicate water samples for analysis of NH₄⁺, NO₃⁻, and SRP were collected from each channel at the downstream end of the pool using a 60-ml syringe and filtered in the field through a syringe filter holder fitted with a Whatman GF/F filter (0.7 µm) and analyzed as described earlier.

At each sample period, three tiles were removed from each channel, as determined by a Latin square experimental design, for analysis of Chl *a* and AFDM. In the laboratory, tiles were scrubbed with a toothbrush to remove epilithon, and scrapings from the three tiles were pooled into one sample per channel and analyzed for Chl *a* and AFDM as described above.

Statistical analyses—Biweekly nutrient and epilithon data from Fish Creek were analyzed by year using repeated-measures analysis of variance (rmANOVA) with location (above or below the salmon barrier) being the independent factor. The time × location interaction was examined to determine whether the two study reaches showed different temporal trends. Tukey's multiple comparison test was used to identify significant differences between the upper and lower reaches at specific sampling times. Relationships between (1) stream discharge and dissolved nutrient concentrations and between (2) epilithon abundance and metabolism were examined using Pearson correlation coefficients (*r*). To analyze trends in nutrients and epilithon across streams, paired *t*-tests were used to assess differences (1) above and below the salmon barrier and (2) before and during salmon runs for all response variables. Each of the six streams was considered a statistical replicate. For the 6-week mesocosm experiment, differences in responses across treatments were analyzed using rmANOVA (SAS, proc mixed model). A Tukey–Kramer test was used to identify particular significant differences within time periods and across treatments. The rmANOVA time × treatment term was used to evaluate whether trends through time differed among treatments. For all analyses, data were square root- or log-transformed when needed to correct for heteroscedasticity and non-normality. SAS v. 8 and SYSTAT v. 10 were used for statistical analyses.

Results

Fish Creek—In 2000 and 2001, patterns in nutrient concentrations were similar in Fish Creek (Fig. 2). During both years, NH₄⁺ concentrations increased 10-fold in the presence of salmon (Fig. 2A,B), and this trend was not observed in the upper (salmon-free) reach during the same time periods (*p* < 0.0001 for both years, rmANOVA time × treatment interaction). In the lower reach, SRP increased during the salmon run by about fourfold in 2000 and sevenfold in 2001 (Fig. 2C,D; *p* < 0.0001 for both years, rmANOVA time ×

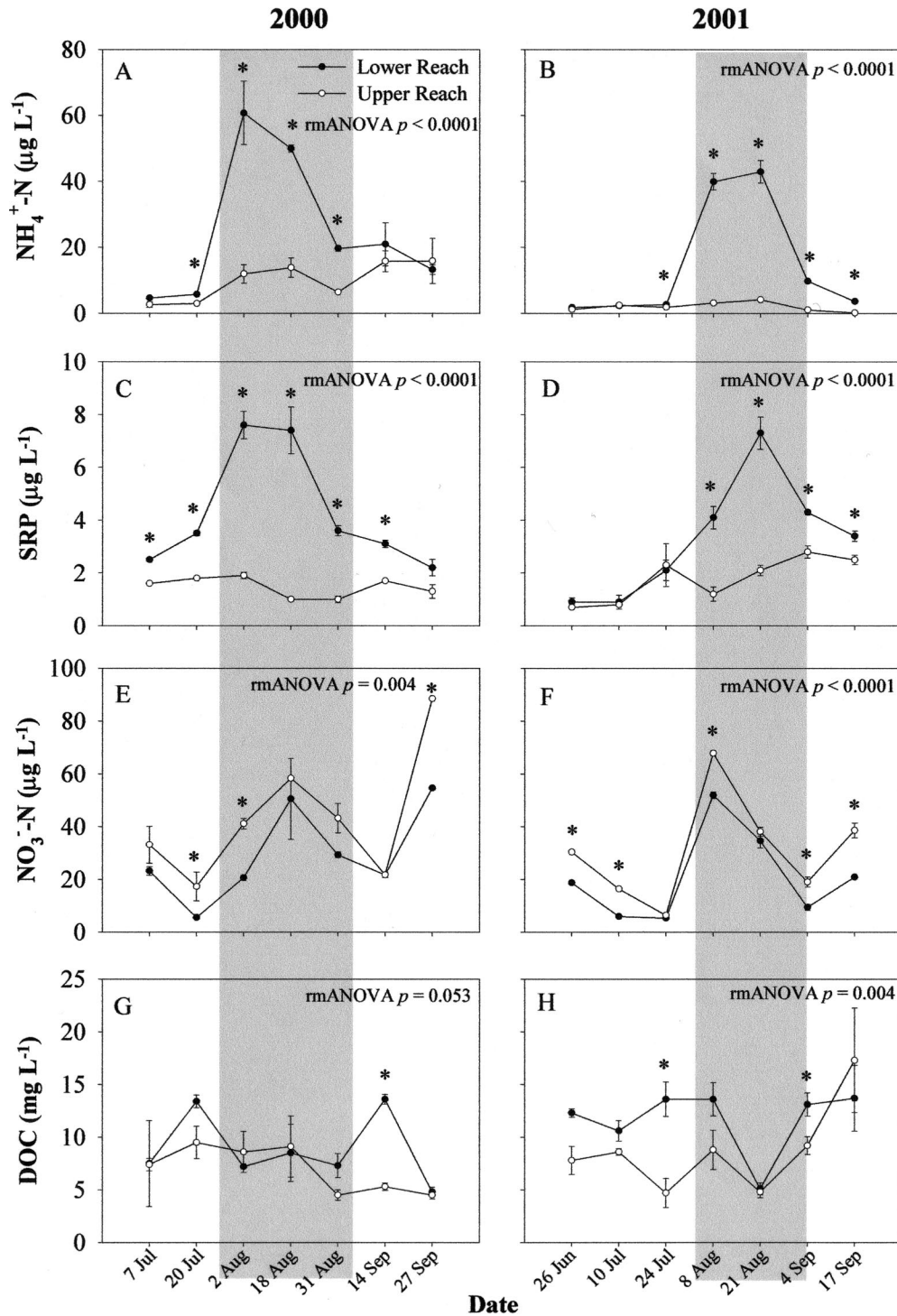


Fig. 2. Surface water concentrations of (A,B) NH_4^+ , (C,D) SRP, (E,F) NO_3^- , and (G,H) DOC in Fish Creek during 2000 and 2001. The shaded sections indicate when spawning salmon and salmon carcasses were present in the stream. The rmANOVA p -value shown is the time \times location interaction. Asterisk indicates significant difference between reaches at specific time points (Tukey's test). Error bars are ± 1 SE.

Table 2. Total mass (kg) of nutrients exported from upper (no salmon) and lower (salmon) reaches of Fish Creek during the 3-month study periods (July–September 2000 and 2001).

	2000			2001		
	Upper Reach	Lower Reach	Estimated contribution from Lower Reach*	Upper Reach	Lower Reach	Estimated contribution from Lower Reach*
NH ₄ ⁺	153.0	427.2	274.2	25.3	232.4	207.1
NO ₃ ⁻	304.7	385.8	81.1	314.4	353.5	39.1
SRP [†]	14.3	70.4	56.1	25.5	68.8	43.3
DOC	0.64×10 ⁵	1.7×10 ⁵	1.06×10 ⁵	1.1×10 ⁵	3.1×10 ⁵	2×10 ⁵

* Calculated as difference between Lower Reach and Upper Reach.

† SRP, soluble reactive phosphorus; DOC, dissolved organic carbon.

treatment interaction). Nitrate concentrations were generally higher in the upper reach than in the lower reach (Fig. 2E,F), and differed significantly between reaches in both years ($p = 0.0042$ in 2000 and $p = 0.0003$ in 2001 rmANOVA time \times treatment interaction). However, variation in NO₃⁻ concentrations did not appear to be influenced by the presence of salmon. Over all sampling dates and at several specific dates, DOC concentrations were significantly higher in the lower reach than in the upper reach (Fig. 2G,H), but as with NO₃⁻, differences did not coincide with the salmon run.

We calculated the total mass of nutrients exported from each reach during the study by estimating the average flux of nutrients between each sampling date and then summing the averages during our entire 3-month study period (Table 2). The difference between the masses of nutrients exported from each reach is approximately the lower reach contribution. In both 2000 and 2001, NH₄⁺, SRP, and DOC contributions from the lower reach were significantly higher than contributions from the upper reach. In contrast, NO₃⁻ export was similar among reaches and years. Discharge in the lower reach was only about 2 \times the discharge in the upper reach; therefore, discharge alone does not account for the large differences in ammonium and SRP export between the two reaches.

We also calculated the mass of salmon nutrients imported (as live fish) and exported (as inorganic nutrients) from Fish Creek in 2001. Import was estimated on the basis of the density and mass of salmon counted each week in the lower reach of Fish Creek and the average wet mass N (3.3%) and P (0.48%) content of southeast Alaska salmon (Gende et al. 2004). Export was based on upstream–downstream flux differences described above. Approximately 427 kg of N and 62 kg of P in salmon tissue entered Fish Creek during 2001; whereas 195 kg of NH₄⁺ and 37 kg of SRP was exported during the salmon run. These mass balance calculations indicate that approximately 46% of salmon nitrogen was exported as inorganic nitrogen and 60% of salmon phosphorus was exported as inorganic phosphorus.

We examined the relationships between nutrient concentrations and discharge in Fish Creek. Ammonium and SRP concentrations were not correlated with discharge (Fig. 3A,B). When salmon were present, elevated levels of NH₄⁺ and SRP relative to discharge were observed in the lower reach but not in the upper reach (encircled points). When salmon were not present, NH₄⁺ and SRP concentrations in both the upper and lower reaches were low and did not vary

with discharge. Nitrate concentrations in both the upper and lower reaches were negatively correlated with discharge (Fig. 3C). In contrast, DOC concentrations were positively correlated with discharge (Fig. 3D).

In 2000, epilithon Chl *a* increased about 20-fold in the lower reach of Fish Creek approximately 2 weeks after the start of the salmon run and remained elevated through the end of the sampling period (Fig. 4A), when no live fish and few carcasses were present. Chl *a* levels in the upper reach remained very low during the same period, and trends through time were significantly different between the lower and upper reaches ($p = 0.0005$, rmANOVA time \times treatment interaction). Epilithon AFDM was more variable than Chl *a* and no significant difference over time was observed between the upper and lower reaches overall (Fig. 4C). However, the overall pattern of AFDM was similar to that of Chl *a*.

In 2001, epilithon Chl *a* in both the upper and lower reaches remained low throughout the study (i.e., maximum of about 20 mg m⁻² compared to 50 mg m⁻² in 2000). Approximately 2 weeks after the start of the salmon run, Chl *a* increased twofold in the lower reach but declined soon thereafter (Fig. 4B). AFDM showed no temporal pattern but was generally higher in the downstream reach both before and during the salmon run (Fig. 4D).

Stream survey—Five additional salmon streams were sampled in 2001 for dissolved nutrients and epilithon above and below a natural fish barrier both before and during the salmon run. In the lower reaches, NH₄⁺ and SRP increased by an average of 10-fold and 3-fold, respectively, from before to during the salmon run (Fig. 5A). Similarly, while the salmon were spawning, NH₄⁺ and SRP concentrations were on average ninefold and threefold greater, respectively, below the salmon barrier than above the barrier (Fig. 5B). There were no significant differences in NO₃⁻, DOC, epilithic Chl *a*, or AFDM either temporally (before vs. during the salmon run; Fig. 5A) or spatially (above vs. below the fish barrier; Fig. 5B). Both Chl *a* and AFDM were strongly correlated with both GPP ($r = 0.777$, $p < 0.001$ and $r = 0.831$, $p < 0.001$, respectively) and NDM ($r = 0.824$, $p < 0.001$ and $r = 0.713$, $p = 0.001$, respectively).

Three sites were sampled in 2001 within the lower reach of each stream to examine longitudinal patterns in dissolved nutrient concentrations. Before the salmon run, no consistent longitudinal patterns in NH₄⁺ or SRP were discernible in the

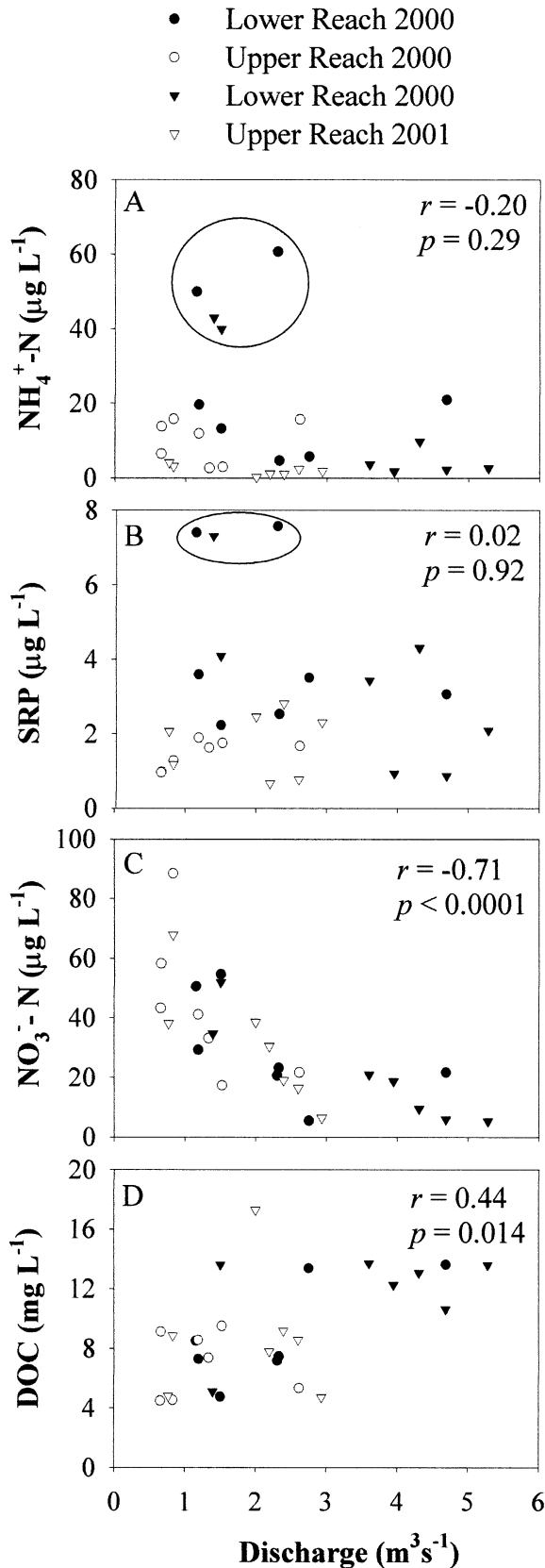


Fig. 3. Relationships between discharge and NH_4^+ (A), SRP (B), NO_3^- (C), and DOC (D) in Fish Creek during the 2-yr study. Encircled points indicate NH_4^+ and SRP concentrations in the lower reach during the salmon run. Pearson correlation coefficients (r) and p -values are given.

lower reaches of the streams (Fig. 6A,B). However, during the salmon run, both NH_4^+ and SRP increased with distance downstream in all streams (Fig. 6C,D).

Mesocosm—Throughout the experiment, NH_4^+ concentrations in HC treatments were significantly higher than NH_4^+ concentrations in LC treatments, and both were significantly higher than in the control (Fig. 7A). At 2 weeks after the start of the experiment, SRP concentrations in the carcass treatments were significantly higher than in the control (Fig. 7B). At 4 weeks, SRP concentrations decreased in carcass treatments and only HC was significantly higher than the control. By the end of the experiment, SRP concentrations did not differ among treatments. During the entire 6-week experiment, NO_3^- concentrations were similar across all treatments, and there was no difference in how the treatments varied over time ($p = 0.259$, rmANOVA time \times treatment interaction). Nitrate concentrations were relatively high (range, 180–240 $\mu\text{g L}^{-1}$) compared to other streams in our study (range, 5–80 $\mu\text{g L}^{-1}$) most likely due to a high concentration of alder trees in the watershed.

Benthic Chl *a* and AFDM increased in all treatments during the experiment. At 2 weeks, Chl *a* and AFDM concentrations were low in all treatments and statistically similar to the control (Fig. 7C,D). At 4 weeks, all treatments including the control had higher Chl *a* and AFDM concentrations than at 2 weeks, and both treatments remained statistically similar to the control. At 6 weeks, differences emerged among treatments. Chl *a* concentrations in LC and HC treatments were three- and fivefold higher, respectively, than the control, and AFDM concentrations in LC and HC were two- and threefold higher, respectively, than the control.

Discussion

Salmon and streamwater nutrients—No previous study has examined the effects of spawning salmon on streamwater nutrients over multiple years and multiple streams. Our study convincingly shows that, across streams in the Juneau area and in mesocosm streams, NH_4^+ and SRP concentrations in streamwater increase on average 10- and 3-fold, respectively, in the presence of spawning salmon, whereas NO_3^- and DOC concentrations do not. Our findings are consistent with some previous short-term studies of dissolved nutrients in Pacific Northwest salmon streams. For example, Brickell and Goering (1970) reported a fivefold increase in NH_4^+ during a salmon run in a stream on Baranof Island, southeast Alaska. Minakawa and Gara (1999) observed a fivefold increase in NH_4^+ and a doubling in SRP, but no change in NO_3^- in a western Washington stream. Sugai and Burrell (1984) observed a fivefold increase in both NH_4^+ and SRP during the spawning season in two southeast Alaska rivers.

The increase in water-column NH_4^+ and SRP during spawning likely was the result of the combination of salmon excretion while alive and tissue decomposition after death. Previous studies have shown that the prominent nutrients in fish excretion are NH_4^+ and SRP (Meyer and Schultz 1985; Brabrand et al. 1990). Furthermore, excreted dissolved organic nitrogen can be rapidly hydrolyzed and mineralized to

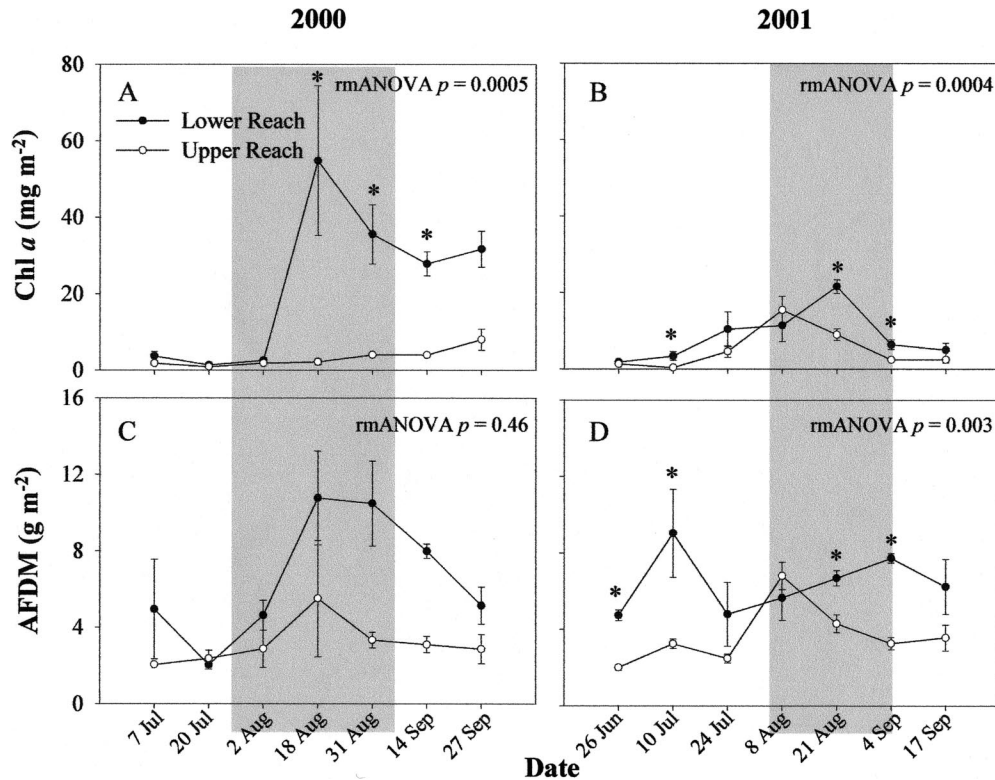


Fig. 4. (A,B) Mean chlorophyll *a* and (C,D) ash-free dry mass of epilithon in Fish Creek during 2000 and 2001. The shaded areas indicate when spawning salmon and salmon carcasses were present in the stream. The rmANOVA *p*-value shown is the time \times location interaction. Asterisk indicates significant difference between reaches at specific time points (Tukey's test). Error bars are ± 1 SE.

NH₄⁺ (Hargreaves 1998). Microbial decomposition of fish carcasses releases organic nitrogen, ammonium, phosphorus, and several micronutrients (Nriagu 1983; Parmenter and Lamarra 1991). Another potential source of NH₄⁺ and SRP during the salmon run (before death) could be a release of nutrients from the interstitial spaces within the streambed due to physical disturbance by the salmon during spawning activity (Tank and Crenshaw unpubl. data).

SRP in the carcass-treated channels of the mesocosm was highest at the beginning of the 6-week experiment and then declined later in the experiment. Kitchell et al. (1975) found that approximately 50% of the phosphorus in bluegill sunfish carcasses was lost within 10 d after death, and the remainder of the phosphorus was bound up in bones and scales. If salmon decompose similarly to sunfish, this could explain why SRP concentrations in the carcass-treated channels declined throughout the experiment. One difference between the natural and artificial streams is that in the natural streams, nutrient release also came from excretion by live spawning salmon. Therefore, it makes sense that we observed a sustained increase in SRP concentrations in the natural streams throughout the salmon run, but in the artificial streams, SRP declined as decomposition of the carcasses progressed.

In contrast to NH₄⁺ and SRP, NO₃⁻ or DOC did not increase when salmon were present. Fish Creek discharge varied from 1.2 to 7.9 m³ s⁻¹ in the lower reach and 0.7 to 4.4 m³ s⁻¹ in the upper reach during the study period. Nitrate concentra-

tion was negatively correlated with discharge, suggesting that NO₃⁻ pools were diluted by increasing discharge and that salmon influence on NO₃⁻ was minor in comparison to discharge. Possible explanations for this pattern include that (1) high-nitrate groundwater input in our study reach was minor compared with surface runoff or direct rainfall input, or (2) high denitrification rates in the groundwater and soils reduced NO₃⁻ concentrations in water entering the stream. In contrast, NH₄⁺ and SRP concentrations were unrelated to discharge, and both increased in the presence of salmon. In the mesocosm streams, discharge was constant throughout the experiment, and we observed no variation in NO₃⁻ concentrations over time or across treatments. Because the main form of nitrogen released from fish carcass decomposition is NH₄⁺ (Hargreaves 1998), we would not expect mesocosm NO₃⁻ concentrations to increase in the carcass treatments unless released NH₄⁺ were nitrified to NO₃⁻.

Epilithon growth in salmon streams—Both Chl *a* and AFDM were strongly correlated with both GPP and NDM; therefore, Chl *a* and AFDM were considered to be reasonable surrogate measures of benthic primary production in these streams. The response in epilithon to the presence of spawning salmon varied between years in one stream (Fish Creek) and across streams during the same year. These results suggest that while spawning salmon increase nutrient concentrations in streamwater, the presence of salmon does not necessarily consistently change epilithon abundance.

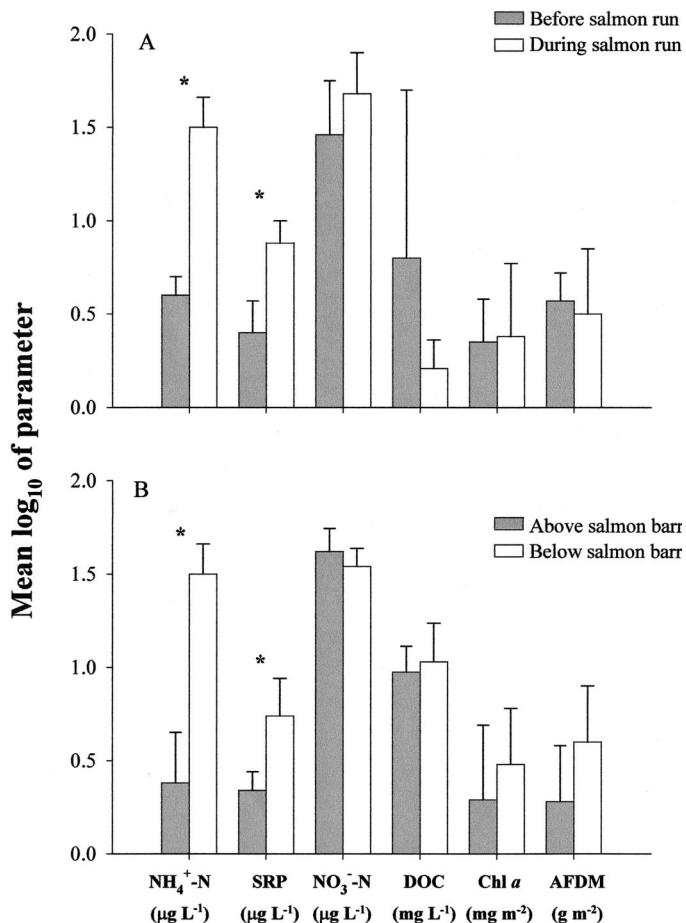


Fig. 5. Mean \log_{10} (+ 1 SE) of concentrations of NH_4^+ , SRP, NO_3^- , DOC, epilithon chlorophyll *a*, and ash-free dry mass (A) before and during the salmon run and (B) above and below a salmon barrier for six southeast Alaska streams. An asterisk indicates a statistically significant difference for groupwise comparisons ($0.05/6 = 0.008$ effective α).

Taken collectively, previous studies also report different responses in epilithon. For example, Wipfli et al. (1998) reported a 15-fold increase in epilithon biomass in a salmon-enriched reach compared to an upstream control reach in a southeast Alaska stream. Schuldt and Hershey (1995) observed a doubling in epilithon Chl *a* below a natural salmon barrier in a Lake Superior tributary stream. In contrast, Minakawa and Gara (1999) found that epilithon algae declined during and after the salmon run in a western Washington stream. Ours is the first study to report that responses can differ in the same stream in different years, and across different salmon streams in the same year.

The discrepancies among previous studies, and the year-to-year and stream-to-stream variation observed in our study, could be related to the density of spawning salmon (Peterson and Foote 2000), time of year of spawning (Peterson and Foote 2000), floods during spawning (Richey et al. 1975), and nutrient or light limitation of epilithon in the stream (Rand et al. 1992). First, spawner density could affect epilithon abundance via two mechanisms: (1) more spawners could increase dissolved nutrient concentrations, which in

turn could increase epilithon, or (2) more spawners could increase physical disturbance of the sediments during redd excavation, and therefore physically reduce epilithon abundance (Minakawa and Gara 1999; Peterson and Foote 2000). From visual estimates, the density of salmon was greater in Fish Creek in 2000 than in 2001. Specifically, the density of chum salmon, which individually contribute a greater mass of organic material and nutrients than pink salmon, was lower in 2001. This could have contributed to the year-to-year variation in epilithon response to spawning salmon in Fish Creek. Second, seasonal variation in physical or chemical factors could be more important than salmon in regulating epilithon abundance in some years. For example, the occurrence of spates during the salmon run could alter the effects of spawning salmon on epilithon abundance because decomposing carcasses could be flushed from the system, therefore depriving the stream of those potential nutrients (Richey et al. 1975). In addition, substrate scouring by spates could override any effects of increased nutrients from salmon. Third, nutrient or light limitation also could modify the effects of salmon-derived nutrients on epilithon abundance. Nutrient-limited streams may respond quite differently to salmon nutrients than streams limited by light availability or some other factor (Lamberti 1996).

The average canopy cover at our Fish Creek sampling sites was about 55% in both the upper and lower reaches. In the lower reach, substantial light reached the channel during most of the day and, when combined with the high water clarity, likely did not limit primary production in Fish Creek during our study (see Lamberti et al. 1989). Additional research is needed to determine whether other factors (e.g., temperature, disturbance, grazing) limit epilithon abundance in Fish Creek, which may help to explain why we saw increased epilithon abundance in response to salmon in one year of our study (2000) but not in the next.

In contrast to the variation in natural streams, we consistently observed increased epilithon growth in carcass-treated channels in the mesocosm experiment. Possible explanations for this discrepancy could be scouring by stream flow in natural streams (Biggs et al. 1999) or physical disturbance of the substrate by salmon redd excavation in natural streams (Peterson and Foote 2000). These disturbances could remove accumulated epilithon from stream substrates, or turn over rocks such that epilithon was deprived of light necessary for algal growth. Responses in epilithon in the mesocosm streams most closely tracked changes in NH_4^+ concentrations. This pattern suggests that, of the parameters measured, NH_4^+ most highly influenced epilithon growth. This outcome is surprising considering the high levels of background NO_3^- in the stream channels that could be used instead of NH_4^+ as a nitrogen source for epilithic organisms. However, organisms that were able to assimilate NH_4^+ as a source of nitrogen might not have been able to use NO_3^- in the absence of other nutrients and micronutrients supplied by carcasses (Syrett 1981). Therefore, perhaps it was not just NH_4^+ that stimulated epilithon growth but rather the combination of NH_4^+ , phosphorus, micronutrients, and organic forms of nutrients that were released from the carcasses.

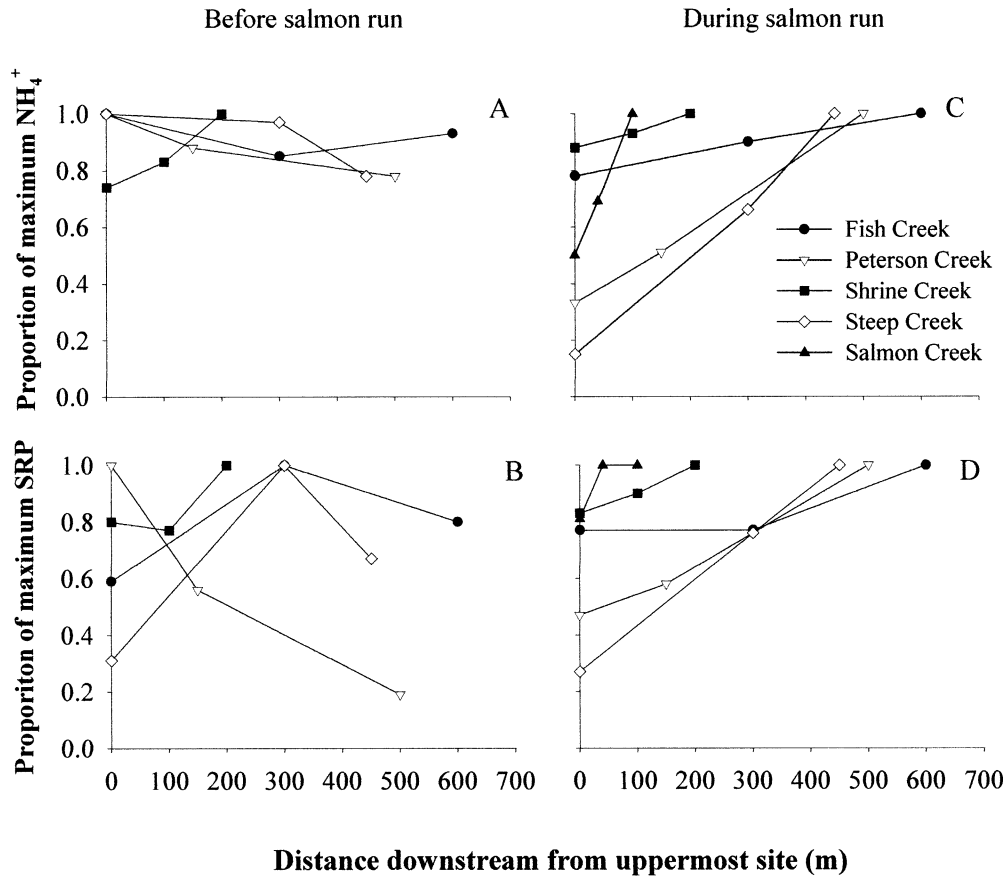


Fig. 6. Longitudinal trends in NH_4^+ and SRP within the lower reach of each study stream (A,B) before and (C,D) during the salmon run. The uppermost site was generally within 100 m of the salmon barrier, and 1.0 represents the site within the lower reach of each stream that had the highest nutrient concentration. Salmon Creek was not sampled before the salmon run.

Nutrient export from salmon streams—In salmon reaches of all streams, NH_4^+ and SRP increased with distance downstream. Brickell and Goering (1970) observed a similar pattern in Sashin Creek, southeast Alaska, during the spawning season. They interpreted the pattern as a loading effect, such that the water furthest downstream had been exposed to more carcasses than the water at the upstream sites. If our Alaskan study streams were nutrient-limited during the salmon run, we would expect to see a longitudinal decline in nutrient concentrations. The pattern of increasing nutrients suggests that nutrient supply was greater than nutrient demand. For Fish Creek, the total mass of NH_4^+ + SRP exported from the lower reach was substantially greater than that exported from the upper reach during the study. This difference was far greater than could be accounted for by increases in discharge. This mass of nutrients, in combination with the longitudinally increasing nutrient concentrations observed in salmon reaches, suggests that a large proportion of marine-derived nutrients are exported back to the estuarine environment in biologically available forms. Our mass balance calculations suggest that 46% and 60% of salmon nitrogen and phosphorus, respectively, were exported from Fish Creek in inorganic forms during one year of our study. These percentages could be an underestimate of the

actual export of salmon nutrients because they do not include organic fractions of nitrogen and phosphorus. In essence, this export completes the cycle of nutrient translocation from salt water to fresh water and back to salt water. Perhaps salmon-derived nutrients are not only ecologically important for freshwater systems but also for the adjacent estuarine and marine environments. Nutrients translocated into fresh water as large organic particles (the bodies of salmon) are redelivered to salt water as inorganic solutes, dissolved organic nutrients, and particulate nutrients that can be readily metabolized.

This study presents spatial (across streams), temporal (over 2 yr), and longitudinal (within a stream reach) evidence that some dissolved nutrients (NH_4^+ and SRP) respond strongly to spawning salmon in southeast Alaska streams. However, other major solutes (NO_3^- and DOC) did not respond to salmon and appear to be more influenced by discharge. The input of MDN from spawning salmon can potentially increase epilithon abundance in nutrient-poor systems, but responses were variable both within and among streams. Other factors, such as light, temperature, disturbance, and grazing, likely also influence epilithon abundance in these streams. Approximately 46% to 60% of salmon-derived nutrients were not retained in fresh water but rather

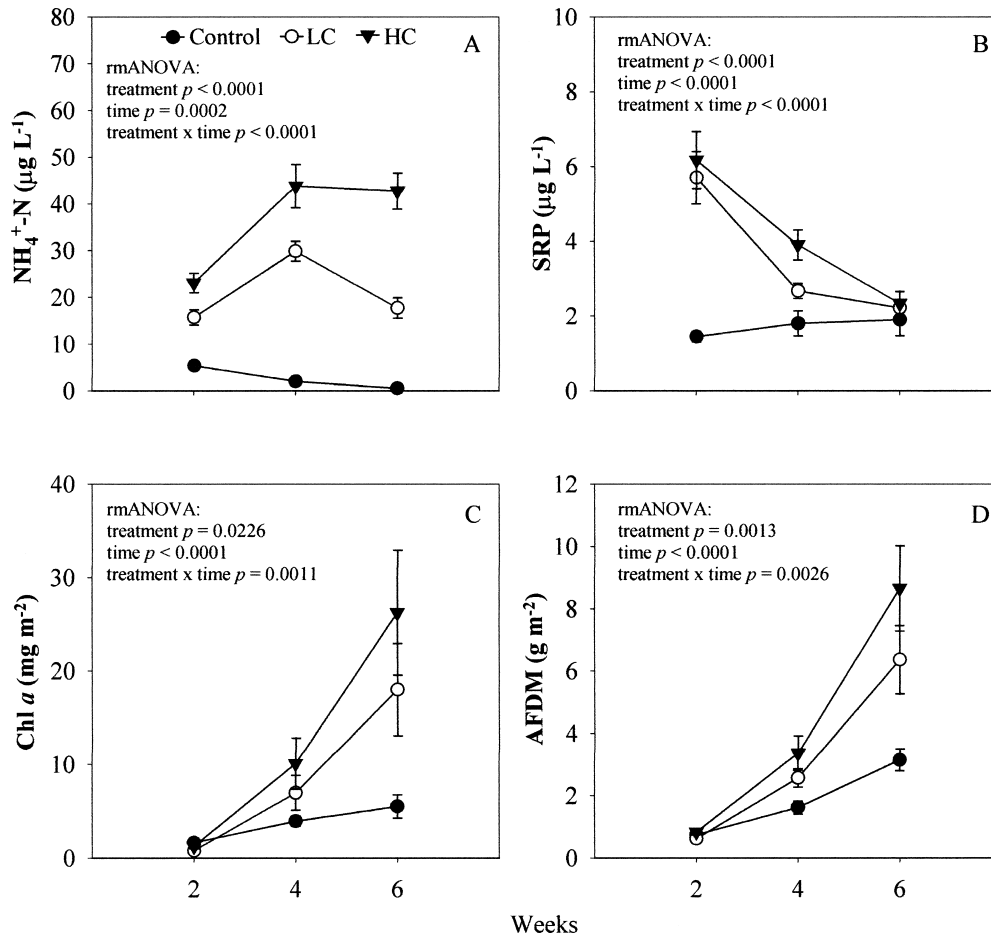


Fig. 7. Mesocosm streamwater (A) NH_4^+ and (B) SRP concentrations and (C) benthic chlorophyll a and (D) ash-free dry mass in mesocosm streams at 2, 4, and 6 weeks after the start of the experiment. Treatments are control (no carcass), low carcass (LC), and high carcass (HC). Letters above bars indicate significant differences (Tukey-Kramer test).

were exported back to the estuarine environment, thus completing a marine-freshwater-marine nutrient cycle. A fuller understanding of the influence of spawning salmon on lower trophic levels will involve exploring pathways of nutrient use by different components of the epilithon and possible changes in community structure elicited by the changing nutrient environment.

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