

Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams

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SUMMARY

1. Pacific salmon are thought to stimulate the productivity of the fresh waters in which they spawn by fertilising them with marine-derived nutrients (MDN). We compared the influence of salmon spawners on surface streamwater chemistry and benthic biota among three south-eastern Alaska streams. Within each stream, reaches up- and downstream of barriers to salmon migration were sampled during or soon after spawners entered the streams.
2. Within streams, concentrations of dissolved ammonium and soluble reactive phosphorus (SRP), abundance of epilithon (chlorophyll *a* and ash-free dry mass) and biomass of chironomids were significantly higher in reaches with salmon spawners. In contrast, biomass of the mayflies *Epeorus* spp. and *Rhithrogena* spp. was significantly higher in reaches lacking spawners.
3. Among streams, significant differences were found in concentrations of dissolved ammonium, dissolved organic carbon, nitrate and SRP, abundance of epilithon, and the biomass of chironomids and *Rhithrogena*. These differences did not appear to reflect differences among streams in spawner density, nor the changes in water chemistry resulting from salmon spawners.
4. Our results suggest that the 'enrichment' effect of salmon spawners (e.g. increased streamwater nutrient concentrations) was balanced by other concurrent effects of spawners on streams (e.g. sediment disturbance). Furthermore, the collective effect of spawners on lotic ecosystems is likely to be constrained by conditions unique to individual streams, such as temperature, background water chemistry and light attenuation.

Keywords: epilithon, macroinvertebrates, Pacific salmon, south-eastern Alaska, water chemistry

Introduction

Ecosystem resource subsidies, in which material moves from donor to recipient systems, are thought to influence some ecosystems strongly (Polis, Ander-

son & Holt, 1997). For example, lotic ecosystems are influenced by terrestrial resource inputs, such as leaf material (Wallace *et al.*, 1999). Another example of an ecosystem resource subsidy is the migration of fish between marine and fresh water (Polis *et al.*, 1997). The ecological importance of these migrations has been underestimated in the past (Willson, Gende & Marston, 1998), and many important questions remain unanswered despite recent advances.

Anadromous Pacific salmon (*Oncorhynchus* spp.) use northern Pacific Rim fresh waters during a critical part of their life cycle (Groot & Margolis, 1991).

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During their upstream migrations to spawn, salmon fertilise streams and adjacent riparian areas with nutrients through excretion, release of gametes and carcass decomposition (Gende *et al.*, 2002; Naiman *et al.*, 2002). Pacific Northwest fresh waters are generally oligotrophic, partly because of the limited availability of either nitrogen and phosphorus, or both (Ashley & Slaney, 1997). Salmon consist of roughly 1% phosphorus and 3% nitrogen (Larkin & Slaney, 1997), so the marine-derived nutrients (MDN) they deliver could constitute a major nutrient subsidy for many Pacific Northwest ecosystems (Gende *et al.*, 2002; Naiman *et al.*, 2002).

Information about the influence of spawning salmon on aquatic systems has accumulated since the work of Juday *et al.* (1932), especially during the last decade (Gende *et al.*, 2002; Naiman *et al.*, 2002). Research has shown that the structure of freshwater ecosystems can be dramatically altered by the presence of salmon spawners, resulting in a widely-accepted paradigm that returning adult salmon increase freshwater productivity (e.g. Naiman *et al.*, 2002). Salmon spawners in general, and salmon tissue specifically, can increase the abundance or biomass of benthic producers and consumers (e.g. Wipfli *et al.*, 1999; Chaloner & Wipfli, 2002) and increase dissolved ammonium and phosphorus concentrations (e.g. Bilby, Fransen & Bisson, 1996; Minakawa & Gara, 1999). Furthermore, stable isotope studies show that salmon can be an important source of nitrogen and carbon for aquatic organisms (e.g. Bilby *et al.*, 1996; Chaloner *et al.*, 2002). However, other than Minakawa & Gara (1999), no study has simultaneously monitored water chemistry and benthic biota in the presence of salmon spawners. Previous MDN studies have also been limited to one or two natural streams (e.g. Wipfli *et al.*, 1999; Peterson & Foote, 2000), although streams and rivers exhibit remarkable spatial heterogeneity in their structure and function at both regional (e.g. Reece & Richardson, 2000) and catchment scales (e.g. Coleman & Dahm, 1990). Better information about the influence of salmon spawners on streams across the landscape would allow a more effective assessment of the 'MDN-enhanced productivity' paradigm (Gende *et al.*, 2002).

The objective of this study was to compare, among three different streams, the responses of benthic epilithon (i.e. microbial assemblages associated with rock surfaces) and epilithic macroinvertebrates to the

presence of spawning Pacific salmon. Our hypothesis was that salmon spawners increase epilithon abundance and epilithic macroinvertebrate biomass in salmon streams, reflecting the increased nitrogen, phosphorus and carbon concentrations in surface streamwater.

Methods

Study sites

The study took place in Fish Creek (58°19'N, 134°35'W), Peterson Creek (58°28'N, 134°44'W) and Salmon Creek (58°19'N, 134°27'W), near Juneau, south-eastern Alaska (Fig. 1). South-eastern Alaska is an area of temperate rainforest with a maritime climate of cool winters and wet summers. Streams are generally warmer than those in the Alaskan interior, with a hydrograph only weakly influenced by snowmelt but strongly influenced by autumn rain (Oswood, Irons & Milner, 1995). The streams used in this study are typical of those found in south-eastern Alaska and similar to each other in many respects, including the presence of waterfalls that are barriers to the upstream migration of salmon (Table 1; Fig. 1). The downstream reaches of all streams have received runs of spawning Pacific salmon (*Oncorhynchus* spp.) for at least the last 20–30 years (Bethers, Munk & Seifert, 1995), and probably for the past 2000–3000 years since the Little Ice Age. Salmon populations in the study streams have all been influenced to some degree by hatchery or stock enhancement programmes [Fish Creek: chinook (*Oncorhynchus tshawytscha* Walbaum) and coho (*O. kisutch* Walbaum); Peterson Creek: pink (*O. gorbuscha* Walbaum), chum (*O. keta* Walbaum), and steelhead (*O. mykiss* Walbaum); Salmon Creek: pink and chum] (Bethers *et al.*, 1995). Apart from the absence of salmon spawners in upstream reaches, both up- and downstream reaches of all streams were similar (e.g. geomorphology, substratum, canopy cover, gradient) (Bethers *et al.*, 1995; Mitchell, 2002).

Spawner density

To estimate spawner density (i.e. the number of adult spawners per unit area), the number of adult salmon was visually counted within a fixed area in each stream, one day per week from 22 July to 14 October,

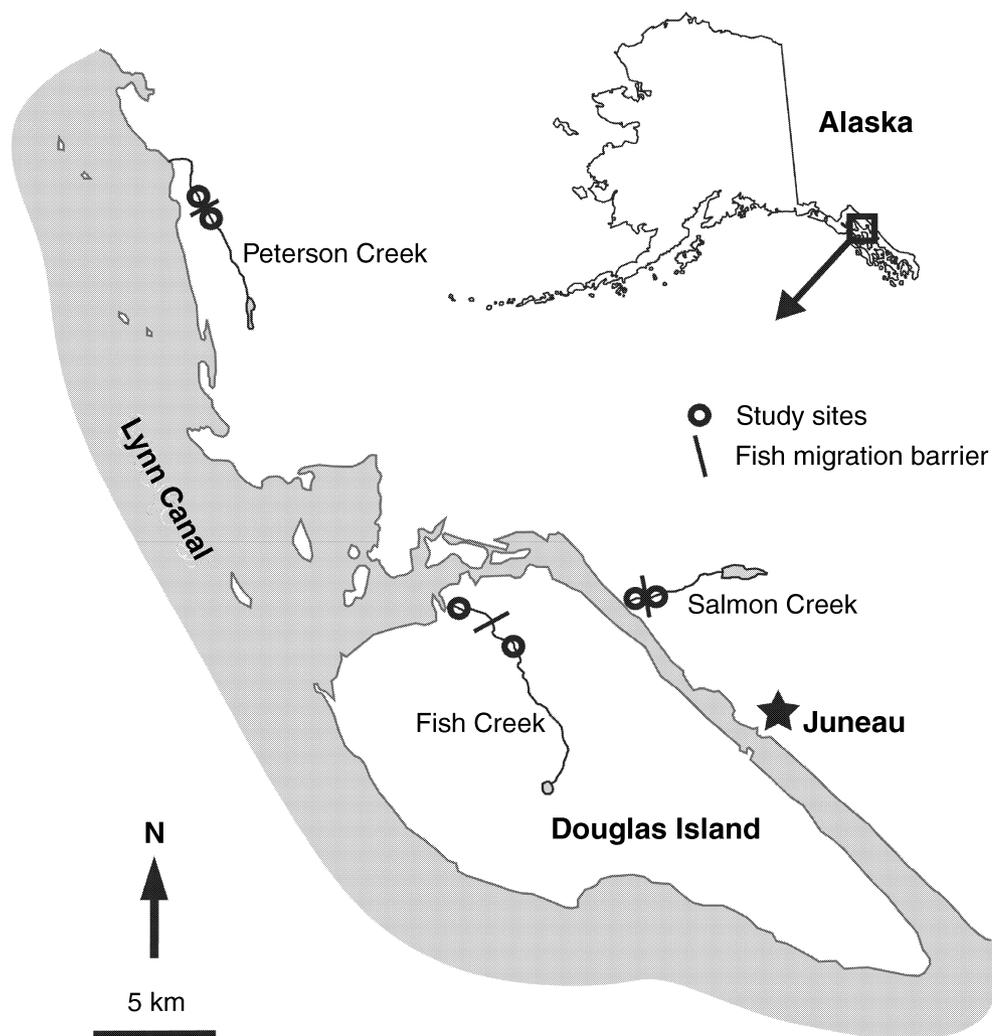


Fig. 1 Location of study streams in south-eastern Alaska, U.S.A.

2001. Numbers were estimated from three separate, demarcated areas in each stream that were similar in area (approximately 50–80 m²) and habitat type (pool-riffle transition area, downstream of large pools). Our approach was a compromise between two commonly-used methods for estimating spawner abundance in streams: counting spawners while travelling the length of a stream (by foot or air) (Bevan, 1961) and counting spawners as they pass a given point in the stream (from a counting tower or using a weir) (Becker, 1962). We used our approach because other methods were not feasible for the length and number of streams studied, and our approach generated estimates of the numbers of fish per unit area rather than numbers of fish per unit length of stream or simply passing a given point.

Surface water chemistry

In each stream, water samples were collected from three different locations (200–300 m apart in Fish Creek, 150–300 m apart in Peterson Creek, and 50 m apart in Salmon Creek) in both upstream (upper; salmon spawners absent) and downstream (lower; salmon spawners present) reaches (Mitchell, 2002). Three replicate water samples were collected at each location. Sampling dates in 2001 were 21 August for Fish Creek, 30 August for Peterson Creek, and 18 August for Salmon Creek, coinciding with the mid-point of the salmon run in each stream. Dissolved nutrient concentrations in the water column were determined for ammonium (NH₄⁺-N) using the fluorometric technique (Holmes *et al.*, 1999), for

Table 1 Characteristics of the three study streams

Stream	Pacific salmon species*	Spawner densities [†] (fish m ⁻²)	Barrier [‡] (km)	Catchment area (km ²)	Discharge [§] (m ³ s ⁻¹)	Water temperature [§] (°C)	Pebble size [¶] (mm)	Oxygen [§] (mg L ⁻¹)	Gradient (%)	Large wood** (pieces km ⁻¹)	Canopy cover ^{§,††} (%)
Fish Creek	CH, CK, CO, PK	0.08 (0.01–0.14)	4	36	4.6 (0.8–13.6)	9.1 (5.3–12.2)	64–128	11.3 (10.1–12.7)	2	333	44 (30–55)
Peterson Creek	CH, CO, PK, SH	0.08 (0.00–0.53)	2	23	2.4 (0.1–8.8)	10.9 (6.4–15.0)	32–64	9.8 (5.9–12.7)	4	416	53 (43–56)
Salmon Creek	CH, CO, PK	0.12 (0.01–0.83)	0.5	26	1.9 (0.6–4.1)	8.4 (5.2–11.4)	32–64	11.4 (10.7–12.5)	6	306	66 (57–74)

*CH, chum (*Oncorhynchus keta*); CK, chinook (*O. tshawytscha*); CO, coho (*O. kisutch*); PK, pink (*O. gorbuscha*); SH, steelhead (*O. mykiss*).

†Running average (range) for the period of the salmon run.

‡Distance from saltwater.

§Average (range); values are for the period June to November.

¶Predominant size class within study reaches.

**Counts of large wood (>1 m in length and >0.1 m in diameter) within study reaches and divided by reach length.

††Estimated using a spherical densitometer.

dissolved organic carbon (DOC) using a Model TOC-5000A high temperature combustion carbon analyser (Shimadzu, Columbia, MD, U.S.A.) for nitrate (NO₃⁻-N) using the hydrazine reduction method (Kamphake, Hannah & Cohen, 1967), and for soluble reactive phosphorus (SRP) using the ascorbic acid method (APHA, 1992).

Epilithon

Similarly, epilithon samples were obtained from three locations in the up- and downstream reaches of each stream (Mitchell, 2002). Sampling locations and dates were the same as for water chemistry. At each site, five individual rocks (mean ± SD diameter: Fish Creek 17.7 ± 0.5 cm, Salmon Creek 17.3 ± 0.5 cm, Peterson Creek 6.1 ± 0.1 cm) were removed haphazardly from riffle habitats. Five rocks were found to be an adequate sample size to provide good estimates of epilithic chlorophyll *a* and ash-free dry mass (AFDM) (N.L. Mitchell, unpublished data). In Fish and Salmon Creeks, a syringe-toothbrush sampler (Steinman & Lamberti, 1996) was used to scrub a round patch (7.1 cm²) from the surface of each rock. In Peterson Creek, rock shapes were too irregular to sample effectively with the syringe-toothbrush sampler and, therefore, rocks were returned to the laboratory in individual bags and the entire rock surface scrubbed using toothbrushes. The rock surface area was estimated by weighing the amount of aluminium foil needed to wrap each rock (Steinman & Lamberti, 1996). Each epilithon sample was analysed sequentially for chlorophyll *a* and AFDM. Chlorophyll *a* was extracted from sample material in 90% buffered acetone for 24 h, measured spectrophotometrically, and then corrected for phaeopigments (APHA, 1992). AFDM of all material was then measured according to Steinman & Lamberti (1996).

Macroinvertebrates

Macroinvertebrates were sampled from individual rocks rather than by sampling a known area of stream bed. According to Scrimgeour, Culp & Glozier (1993), this method is effective for sampling epilithic macroinvertebrates from the coarser substratum (≥180 mm diameter) present in our study streams (Table 1). This method may not effectively sample highly mobile taxa (e.g. baetid mayflies), but this would be consistent

among sites and samples. Rocks were selected haphazardly from a riffle in the upper and lower reaches of each stream. Sampling dates in 2001 were 17 September for Fish Creek, 20 September for Peterson Creek and 18 September for Salmon Creek, at which time live salmon spawners were no longer observed in the stream. Macroinvertebrate sampling took place several weeks after epilithon sampling because the lag time in response was expected to be longer for macroinvertebrates than epilithon. Five rocks of similar size (mean diameter $18.3 \text{ cm} \pm 0.3 \text{ cm}$) were collected from each stream reach using a modified D frame-net (250 μm mesh) as described by Scrimgeour *et al.* (1993). Placing a net downstream before and during rock removal minimised the escape of highly mobile taxa. Each rock was individually scrubbed with a soft toothbrush in a large pan while frequently rinsing with stream water. Accumulated water was poured through a 250- μm sieve, and trapped material preserved with 95% EtOH. Rock surface area was estimated using the aluminium foil method (Steinman & Lamberti, 1996). In the laboratory, all macroinvertebrates were sorted from each sample, except for the numerous chironomids (Diptera: Chironomidae), which were counted from a sub-sample of one quarter of the original. Macroinvertebrates were identified to genus or family using the keys of Merritt & Cummins (1996) and the body length of all individuals was measured ($\pm 1 \text{ mm}$). Macroinvertebrate dry mass was estimated from lengths using established length–mass equations (e.g. Benke *et al.*, 1999; Sabo, Bastow & Power, 2002).

Statistical analyses

We compared lower reaches (downstream of the barrier) that contained salmon spawners to upper reaches (upstream of the barrier) lacking salmon spawners, nested within three streams ($n = 3$). Within each stream reach, the three sample locations were considered subsamples (d.f. = 8). Response variables were dissolved concentrations of major nutrients (ammonium, DOC, nitrate and SRP), epilithon abundance (chlorophyll *a* and AFDM), and macroinvertebrate dry mass (total mass of all taxa combined and individual taxa representing $\geq 5\%$ of the total mass). Because reaches were not independent of streams, a two-way factorial nested analysis of variance (ANOVA) was used to determine whether stream

and reach differences were significant. Data that violated the assumptions of ANOVA were transformed (log, square-root or arcsine square-root) and analysed using a general linear model (PROC GLM, SAS Institute, 2000). Where ANOVA indicated no significant interaction between streams and reaches, Tukey's HSD test was used to establish which streams were different. We used a sequential Bonferroni technique (Dunn-Šidák method, $\alpha = 0.05$) to limit our procedure-wise error rate (Sokal & Rohlf, 1995).

Results

Spawner density

Overall, spawner density was within the range reported for pink and chum salmon in streams (Groot & Margolis, 1991). Spawner density differed among the three streams (Table 1), with the highest density occurring in Salmon Creek (in terms of both the absolute value and the running average) (Fig. 2c) and the lowest in Fish Creek (Fig. 2a). Pink and chum salmon in Salmon Creek were probably augmented by individuals that strayed into the stream from a commercial salmon hatchery <1 km away (Bethers *et al.*, 1995). Similarly, the run of wild chum salmon into Peterson Creek was augmented by hatchery fish originally released as juveniles close to the mouth of that stream. The small number of salmon spawners (1000–2000) that returned to Fish Creek in 2001 was less than the average of more than 9000 (maximum about 30 000) that had returned in previous years (Bethers *et al.*, 1995). Timing of the salmon run also differed somewhat among the three study streams. Salmon spawners first appeared in Salmon Creek on 4 July, whereas no salmon were observed in Peterson or Fish Creeks until 22 July. Live salmon spawners were present in Salmon Creek for the longest period (approximately 13 weeks) and in Fish and Peterson Creeks for a shorter period (approximately 9 weeks). Salmon spawner dynamics differed among the three streams. Peterson Creek appeared to be the most variable (Fig. 2b) and Fish Creek the least (Fig. 2a). The large variation in spawner density in Peterson Creek reflected a massive die-off over a relatively short time period from 5 August to 19 August, because of a combination of high spawner density, low discharge, high water temperature and low dissolved oxygen (Table 1).

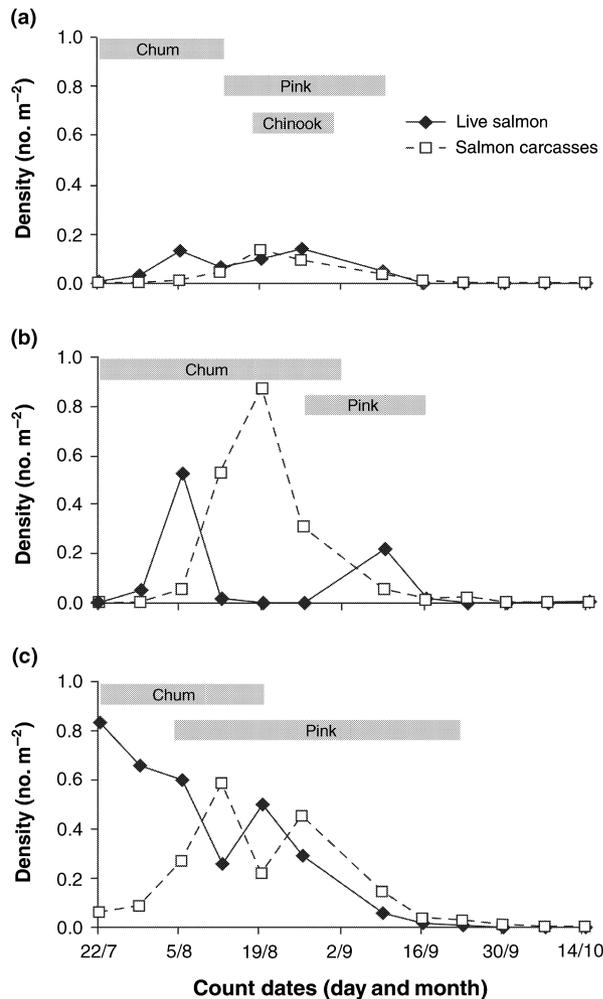


Fig. 2 Density of salmon spawners and carcasses over time in the three study streams, Fish Creek (a), Peterson Creek (b) and Salmon Creek (c). Labelled bars above each graph indicate the periods that individual salmon species were present.

Surface water chemistry

Ammonium and SRP concentrations were significantly higher in stream reaches containing salmon spawners than in reaches lacking spawners ($P < 0.002$; Fig. 3), whereas nitrate and DOC did not differ between stream reaches. Ammonium, DOC, nitrate and SRP concentrations differed significantly among streams ($P < 0.013$; Fig. 3). Ammonium and SRP background concentrations (i.e. in upper reaches) did not differ among the three streams, whereas DOC and nitrate concentrations differed markedly. The high DOC in Peterson Creek reflected the dark, humic-stained waters of this stream. Among the three streams, the presence of salmon spawners increased

ammonium the most in Peterson Creek and increased SRP the most in Fish Creek.

Epilithon

Epilithic chlorophyll *a* and AFDM were both significantly higher in stream reaches containing salmon spawners ($P < 0.01$; Fig. 4) and also differed significantly among streams ($P < 0.001$; Fig. 4). Salmon Creek exhibited the largest difference between reaches in both chlorophyll *a* and AFDM. Overall, epilithon was much more abundant in Fish and Salmon Creeks than in Peterson Creek.

Macroinvertebrates

Total macroinvertebrate biomass did not differ significantly between the two reaches of each stream (Fig. 5a). Of the individual taxa analysed, only the biomass of chironomids was significantly higher in stream reaches containing salmon spawners ($P < 0.001$; Fig. 5b). In contrast, the biomass of other taxa was either significantly higher ($P < 0.01$) in reaches lacking spawners [e.g. *Epeorus* spp. (Ephemeroptera: Heptageniidae), *Rhithrogena* spp. (Ephemeroptera: Heptageniidae); Fig. 5e,f] or did not differ significantly between reaches [e.g. *Baetis* spp. (Ephemeroptera: Baetidae), *Drunella* spp. (Ephemeroptera: Ephemerellidae), Fig. 5c,d]. Among streams, total biomass and individual biomass of chironomids and *Rhithrogena* spp. varied significantly ($P < 0.015$; Fig. 5b,f; Table 2), and was lowest in Peterson Creek. Chironomids contributed, on average, the largest proportion of epilithic macroinvertebrate biomass (25% of total biomass; Table 2) while *Epeorus* and *Rhithrogena* contributed 12% and 17% of total biomass, respectively (Table 2). Of all the contrasts, only the biomass of chironomids exhibited a significant interaction ($P < 0.01$; Fig. 5b) between streams and reaches, probably driven by the very low biomass in Peterson Creek compared with the other streams.

Discussion

Responses of benthic biota to salmon spawners

Epilithon and some epilithic macroinvertebrates responded to the presence of salmon spawners.

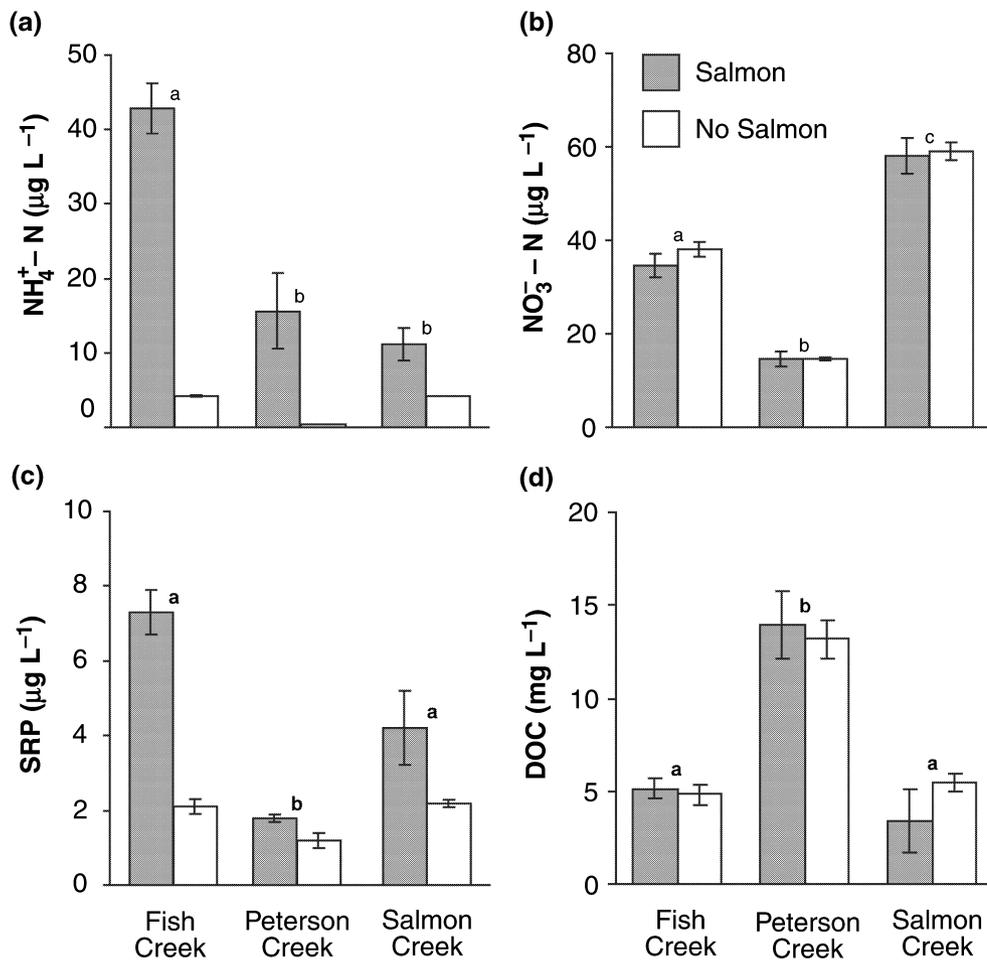


Fig. 3 Concentrations of dissolved ammonium (a), nitrate (b), soluble reactive phosphorus (c) and dissolved organic carbon (d) in reaches of the three study streams with and without salmon spawners. Lower case letters indicate streams that were significantly different according to Tukey's HSD test (streams sharing the same letter are not different). Error bars represent ± 1 SEM.

Epilithon was generally more abundant in stream reaches fertilised by salmon spawners, but the magnitude of this difference varied among the three study streams. Previous studies (e.g. Warren *et al.*, 1964; Mundie, Simpson & Perrin, 1991; Wipfli *et al.*, 1999) suggest that epilithon abundance responds to both the quantity and type (e.g. sucrose, inorganic nutrients, carcasses) of material added to a stream. However, large standing crops of epilithon are often unstable and subject to sloughing, thereby limiting potential responses to increased nutrient availability (e.g. Lamberti *et al.*, 1989; Wipfli *et al.*, 1999). Nevertheless, substantial variation in epilithon abundance was found among streams. Differences in spawner density could explain the higher epilithon abundance in Salmon Creek compared with Peterson Creek but cannot explain the higher abundance of epilithon in

Fish Creek compared with Peterson Creek. Similarly, epilithon abundance did not always track the changes or differences in dissolved nutrient concentrations. We propose that variation in the epilithon abundance among streams was primarily related to the physiochemical background of each stream and only secondarily to salmon spawner abundance. For example, the dark, humic-stained water of Peterson Creek probably attenuated the light reaching the epilithon much more than the clearer water of Fish and Salmon Creeks. A reduction in light, and thus autotrophic production, should increase the Autotrophic Index (AI, ratio of AFDM to the amount of chlorophyll *a*; Steinman & Lamberti, 1996). Indeed, epilithon in Peterson Creek (mean AI = 1313) was much more heterotrophic than in Salmon Creek (mean AI = 275) or Fish Creek (mean AI = 310).

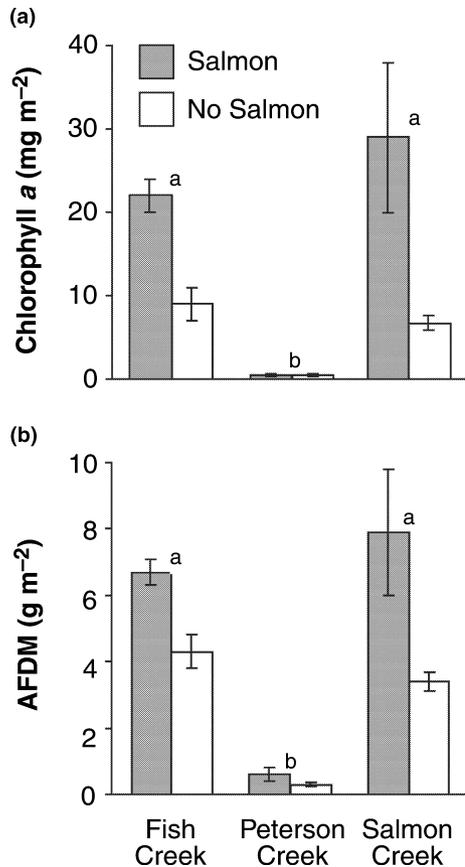


Fig. 4 Epilithon chlorophyll *a* (a) and ash-free dry mass (b) in reaches of the three study streams with and without salmon spawners. Lower case letters indicate streams that were significantly different according to Tukey's HSD test (streams sharing the same letter are not different). Error bars represent ± 1 SEM.

Chironomids were the only macroinvertebrates whose biomass appeared to be stimulated by the presence of salmon spawners, and whose response tracked epilithon abundance in each stream. In previous studies, chironomids responded positively to the addition to streams of organic and inorganic material (e.g. Warren *et al.*, 1964; Mundie *et al.*, 1991) including salmon carcasses (e.g. Wipfli *et al.*, 1999). The dramatic response by chironomids to nutrient enrichment probably reflects their exceptional dispersal ability, rapid reproduction and development, and broad food and habitat preferences (Armitage, Cranston & Pinder, 1995). Chironomids may recolonise salmon reaches during a small 'window of opportunity' between the end of salmon sediment disturbance, and the declining light and water temperature that are likely to limit in-stream primary production in the Pacific Northwest (Bisson & Bilby, 1998). Chirono-

mids are important food web members because of their high rates of secondary production and contribution to the diet of many predators, including juvenile salmonids (Armitage *et al.*, 1995). In this way, chironomids may significantly influence the uptake, trophic transfer and, ultimately, retention of MDN in salmon streams.

The biomass of most other epilithic macroinvertebrates was either reduced or unaffected by the presence of salmon spawners despite increased epilithon abundance, the putative food source for many riffle invertebrates (Lamberti, 1996). The most plausible explanation is that populations of most invertebrate taxa were initially reduced by salmon spawner disturbance, but only chironomid populations recovered during the weeks between the end of the salmon run and our sampling. Competitive exclusion of other invertebrate taxa by chironomids in downstream reaches seems unlikely, especially given that mayfly larvae in upstream reaches, a likely source of colonists, were larger (length >4 mm) than most chironomid larvae (length <2 mm). Differences in predation pressure may also be a factor because benthic-feeding predatory fishes, especially sculpins (*Cottus* spp.), can be restricted by waterfalls to the lower reaches of streams (B.E. Wright, USDA Forest Service, personal communication). We also may have underestimated the importance of some macroinvertebrate taxa because of the timing or location of sampling. For example, we expected the collector-gatherer *Baetis* to respond strongly to salmon spawners based on the results of some previous nutrient enrichment experiments (e.g. Mundie *et al.*, 1991; Wipfli *et al.*, 1999). However, if *Baetis* biomass was increased by MDN enrichment, this response occurred after we sampled these streams. Similarly, previous studies indicate that the stonefly shredder *Zapada* helps incorporate MDN into stream food webs (e.g. Wipfli *et al.*, 1999; Chaloner *et al.*, 2002; Chaloner & Wipfli, 2002). In our study streams, *Zapada* larvae were probably most abundant in depositional habitats that we did not sample.

Ecosystem disturbance by salmon spawners

Most studies of the influence of returning salmon on freshwater ecosystems have focused on whether MDN increases the abundance, biomass or growth of various species (e.g. Wipfli *et al.*, 1999; Chaloner &

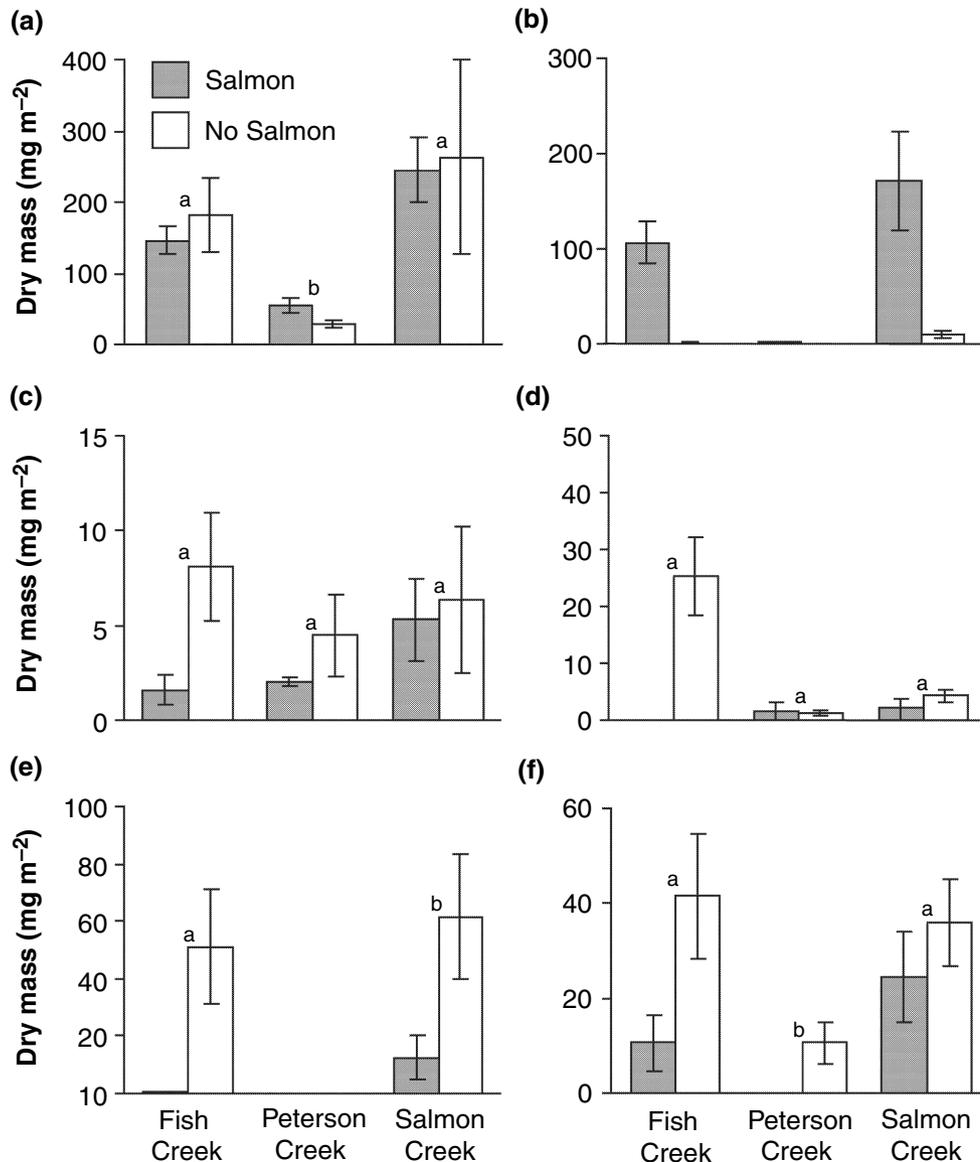


Fig. 5 Estimated dry mass of all taxa combined (a), Chironomidae (b), *Baetis* spp. (c), *Drunella* spp. (d), *Epeorus* spp. (e) and *Rhithrogena* spp. (f), in reaches of the three study streams with and without salmon spawners. Lower case letters indicate streams that were significantly different according to Tukey's HSD test (streams sharing the same letter are not different). No letters are included for Chironomidae because the interaction between stream and reach was significant. Error bars represent ± 1 SEM.

Wipfli, 2002; Mitchell, 2002). In our study, the biomass of several riffle invertebrates was reduced in the presence of salmon spawners. Adult salmon physically disrupt the streambed when they create spawning redds (Montgomery *et al.*, 1996; Peterson & Foote, 2000), and can dramatically reduce dissolved oxygen and increase dissolved ammonium concentrations (Murphy, 1985; Peterson & Foote, 2000). Such effects can be severe when discharge is low and water

temperature and spawner density high, and constitute a disturbance event (Resh *et al.*, 1988). In the Pacific Northwest, floods and salmon spawners may impose similar, seasonal physical impacts on streams in the late summer to early autumn. This temporal coincidence may minimise the long-term impacts of spawner disturbance by favouring disturbance-adapted communities dominated by opportunistic taxa such as chironomids (Armitage *et al.*, 1995). Such

Response	Functional feeding group	Dry mass* (mg m ⁻²)	Relative dry mass* (%)
Insecta			
Ephemeroptera			
Baetidae			
<i>Baetis</i> spp.	c-g, sc	4.7	4.7
Heptageniidae			
<i>Epeorus</i> spp.	c-g, sc	20.9	12.9
<i>Rhithrogena</i> sp.	c-g, sc	20.5	17.7
Ephemerellidae			
<i>Drunella</i> sp.	sc, p	5.8	4.6
Other Ephemeroptera [†]	c-g, sc	5.1	12.0
Plecoptera			
Nemouridae			
<i>Zapada</i> spp.	sh	1.4	1.2
Chloroperlidae [‡]	p, c-g	6.0	8.4
Other Plecoptera [§]	sh, p	1.2	0.9
Trichoptera [¶]	several	33.1	8.8
Diptera			
Chironomidae	several	48.3	25.1
Other Diptera ^{**}	several	6.1	3.6
Arachnida			
Acari	om	<0.1	<0.1
Annelida			
Oligochaeta	c-g	0.1	0.1
All taxa combined		153.3	100.0

*Averaged across both reaches and all streams.

[†]*Ameletus*, *Caudatella*, *Cinygmula*, *Paraleptophlebia*.

[‡]*Kathroperla*, *Sweltsa*.

[§]*Despaxia*, *Taenionema*, *Visoka*.

[¶]*Ecclisomyia*, *Glossosoma*, *Parapsyche*, *Rhyacophila*.

^{**}*Antocha*, *Dicranota*, *Oreogeton*, *Simulium*.

taxa, in turn, may be crucial for the rapid incorporation and efficient retention of MDN into stream food webs. Overall, spawner-mediated disturbance is likely to be important ecologically, but isolating the effects of spawners from those of other natural disturbance events could be challenging.

Implications of salmon-biota interactions for stream ecosystems

Our study has provided two important insights into the interactions between spawning salmon and the benthic biota of streams. The first relates to the considerable stream-to-stream variation in the biotic responses to salmon spawners. This variation is consistent with the large heterogeneity in structure and function often found among streams (e.g. Coleman & Dahm, 1990; Reece & Richardson, 2000). Global assumptions about influence of salmon spawners on streams (e.g. the 'MDN-productivity para-

digm') cannot be made. Characteristics of individual streams or catchments are likely to modulate the overall influence of spawning salmon on stream biota. Our results suggest that shading from DOC-stained water or riparian canopy can constrain the epilithon response to MDN, although Wipfli *et al.* (1999) described several other abiotic factors (e.g. habitat area) that could vary among streams and similarly constrain biotic responses. Biological characteristics of streams, such as community resistance or resilience to disturbance, may also modify the overall influence of salmon spawners on streams (Wipfli *et al.*, 1999).

The second important insight from our study was the potential importance of disturbance as a mechanism by which salmon influence streams. The broad role of disturbance in food web dynamics has been recognised and explicitly linked to consumer-resource interactions in stream communities (e.g. Wootton, Parker & Power, 1996). One important issue is whether aquatic organisms can cope with the predict-

Table 2 Functional feeding group (c-g, collector-gatherer; om, omnivore; p, predator; sc, scraper; sh, shredder; after Merritt & Cummins, 1996), mean actual dry mass, and mean percent relative dry mass of epilithic macroinvertebrates

able, annual disturbance associated with spawning salmon, and whether the stream community as a whole is therefore more resilient to disturbance. The dominance of chironomid larvae in salmon reaches may simply reflect their life history characteristics that adapt them to disturbance events. Alternatively, the stream community as a whole may be pre-adapted to disturbance as a result of flooding, and this adaptation may partly explain why lotic ecosystem of the Pacific Northwest supported large populations of Pacific salmon.

Salmon-mediated disturbance and the spatial variation in responses to salmon have important implications for future Pacific salmon management plans. Past salmon restoration efforts have concentrated on restocking and nutrient enrichment (Ashley & Slaney, 1997). Future management plans should consider that one management prescription may not apply to all catchments, especially when physicochemical conditions (e.g. background nutrient concentrations, geomorphology, hydrology) of individual streams vary widely. Disturbance by floods may be critical for maintaining a community able to exploit MDN delivered by spawning salmon. Chironomids are likely to be important components of that community because they can rapidly develop large populations able to capitalise upon MDN enrichment before reductions in light and water temperature. Widespread streamflow regulation, which many believe already hinders salmon recovery by obstructing fish movement (Wootton *et al.*, 1996), may have compromised the ability of stream communities to cope with disturbance and to use MDN delivered by spawning salmon.

We have shown that Pacific salmon spawners can alter the concentration of certain dissolved nutrients and the abundance or biomass of some freshwater organisms. Changes in the quality or quantity of streamwater nutrients, animal detritus or benthic producers can initiate a 'bottom-up' trophic response, potentially influencing all trophic levels in streams. However, the responses of aquatic organisms to nutrient inputs can be constrained by 'top-down' trophic interactions (e.g. predation, herbivory) and abiotic factors (e.g. light, hydrology). Similarly, our results suggest that, although MDN can produce 'bottom-up' effects, other factors complicate or obscure linkages between enrichment, as indicated by spawner density or changes in dissolved nutrient

concentrations, and biotic responses, such as epilithon or macroinvertebrate abundance. Complicating factors include the simultaneous effects of salmon runs (e.g. nutrient enrichment, disturbance) and the abiotic (e.g. light, temperature) and biotic (e.g. community resilience, nutrient uptake) characteristics of each stream. The interaction of these factors probably produces broad variation in the biotic responses to salmon spawners across the Pacific Northwest. Such variability in responses also means that previous studies of MDN at the reach scale need to be verified by studies at broader scales. Furthermore, resource managers developing restoration strategies for salmon in the Pacific Northwest should consider how the conditions of individual catchments can modulate the influence of nutrient enrichment on freshwater ecosystems and other consequences of anadromous salmon.

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