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Investigating the effect of marine-derived nutrients from spawning salmon on macroinvertebrate secondary production in southeast Alaskan streams

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Abstract. It is generally accepted that juvenile salmonid production is linked, via bottom-up pathways, to marine-derived nutrient (MDN) inputs from spawning salmon. Many studies have used standing stock biomass estimates of aquatic macroinvertebrates to infer relationships between MDN and secondary production in streams that receive spawners. However, no study has measured aquatic macroinvertebrate secondary production in relation to MDN. To assess the relationship between MDN and aquatic insect production, we measured secondary production of the 5 dominant mayfly genera (*Baetis* spp., *Drunella* spp., *Cinygmula* spp., *Epeorus* spp., and *Rhithrogena* spp.) and chironomids throughout the primary growing season in 2 streams in southeastern Alaska. Both streams had upstream reaches blocked from spawning salmonids by a waterfall barrier and downstream reaches that received large spawning runs of pink and chum salmon. Four of the mayfly genera studied (*Drunella* spp., *Cinygmula* spp., *Epeorus* spp., and *Rhithrogena* spp.) had significantly greater production in upstream than in spawning reaches. Secondary production of *Baetis* spp. was similar between upstream and spawning reaches. Chironomid production was significantly greater in spawning than in upstream reaches. However, biomass of each taxon was maximized in the spring and summer before the primary period of MDN input. These patterns indicate that another factor, primarily spawning disturbance, is an important driver of benthic insect secondary production in these streams and might provide the community structure within which MDN subsidies occur. If these patterns are common in streams that receive salmon runs, then secondary production-mediated links between MDN and juvenile salmonid production might be mostly the result of responses of chironomids and other benthic organisms with similar life histories.

Key words: mayflies, chironomids, disturbance, nutrient subsidy, life history.

Nutrient transfers in lotic systems occur in a variety of ways, and their importance is crucial to understanding the dynamics of ecosystem productivity. A well-known example is the use and transfer of terrestrially derived nutrients (e.g., leaf litter) from headwaters to downstream areas (Kaushik and Hynes 1971, Cummins 1974, Vannote et al. 1980, Cummins et al. 1989). Nutrients also are transferred from marine systems into freshwater via fish migrations (Polis et al. 1997, Cederholm et al. 1999, Gresh et al. 2000). Coastal streams that are spawning grounds for salmon receive these nutrients, termed marine-derived nutrients (MDN), in the form of salmon eggs, sperm, metabolic waste, and adult carcasses (Cederholm et al. 1999). MDN transfers from adult salmon might offer a positive feedback mechanism for juvenile salmonid production (Kline et al. 1997, Lichatowich 1999). However, most research on this phenomenon has focused either on tracing MDN through surface-stream and riparian food webs or on short-term comparisons of stream communities with and without salmon (Bilby et al. 1996, Kline et al. 1997, Wipfli et al. 1998, Cederholm et al. 1999, Chaloner et al. 2002a). The importance of MDN subsidies to stream ecosystem productivity and

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juvenile salmon survival is of particular interest in the Pacific Northwest of the US, where natural salmon runs are extinct or threatened in many streams along the coasts of Washington, Oregon, and California.

A basic tenant of MDN theory is that salmon-mediated MDN provides an essential nutrient source to the typically oligotrophic streams of the Pacific Northwest region and increases stream productivity and the viability of salmonid offspring by subsidizing the nutrient base in spawning grounds (Kline et al. 1997, Lichatowich 1999). Ample evidence shows incorporation of nutrients from spawning salmon into stream communities (Schuldt and Hershey 1995, Bilby et al. 1996, Chaloner et al. 2002a, Claeson et al. 2006) and perceptible stimulation of primary production and standing stock of certain fauna (e.g., chironomids) (Kline et al. 1997, Wipfli et al. 1999, Chaloner et al. 2002a, Lessard and Merritt 2006). However, the influence of MDN on the long-term productivity of these streams remains unclear. In fact, many studies discuss the implications of their results in terms of production, but the influence of MDN on secondary production (i.e., accrual of biomass over time) has yet to be measured (Gende et al. 2000, Lessard et al. 2003, Lessard and Merritt 2006, Moore and Schindler 2008).

Alaska is one of the few areas in the US where salmon runs remain at or near historic levels (Baker et al. 1996, Gresh et al. 2000). Southeast Alaska's 8.5-million-ha Tongass National Forest has 5200 anadromous salmon streams that collectively support millions of spawning salmon (e.g., annual transport of >100 million kg C, 10 million kg N, 2 million kg P, and other nutrients to freshwater streams) (Halupka et al. 1999, Gresh et al. 2000). Our objective was to quantify secondary production of selected aquatic insects to evaluate the influence of MDN on their annual production in these systems. Because we worked in Alaskan streams, we were able to take advantage of the relatively pristine state of the MDN transfer cycle that remains in streams in this region. We also took advantage of the fact that southeastern Alaska has many streams with reaches open to the marine environment that provide spawning habitat for annual migrations of salmon, but that also have natural waterfalls that block salmon from reaches further upstream (i.e., natural control).

We hypothesized that for MDN to be of real importance to overall stream productivity, MDN subsidies would have to be retained long enough and in large enough quantities to elicit a bottom-up response from the fauna. Specifically, we hypothesized that if MDN provides an important nutrient subsidy to these streams, then aquatic insects living below the waterfall barriers (i.e., with MDN in the system) would have higher secondary production rates than aquatic insects living above the barriers (i.e., without MDN). To understand the way in which MDN influences secondary production of different types of insects, we selected insects that are common and abundant in southeast Alaskan streams and that have varied life histories (Table 1).

Study Area

Fish Creek (lat 58°19′N, long 134°35′W) and Salmon Creek (lat 58°19′N, long 134°27′W) are streams that support anadromous fishes in the Juneau–Douglas area in southeast Alaska (Fig. 1). Both streams are characterized by the cool, clear, oligotrophic appearance typical of forested streams in the Pacific Northwest. Fish Creek (watershed area = 36 km^2) is on Douglas Island and receives annual runs of salmon (*Oncorhynchus*), including chum (*O. keta*), chinook (*O. tshawytscha*), coho (*O. kisutch*), and pink (*O. gorbuscha*). The largest runs are the pink and chum spawning migrations, which normally take place between late July and September. Salmon Creek (watershed area = 26 km^2) is near downtown Juneau and receives pink, chum, and coho salmon. The largest runs are the pink and chum spawning migrations. Both streams have natural waterfall barriers that block salmon migration into upstream reaches (Fig. 1). Stream habitat and riparian condition are similar in upper and lower reaches in both study streams (Lessard and Merritt 2006) (Table 2).

Methods

Samples of benthic macroinvertebrates were collected with a modified Hess sampler (0.04 m^2, mesh size = 250 μm). Benthic samples were collected in each stream approximately every 2 wk from May to September 2002 (18 May, 14 June, 29 June, 12 July, 28 July, 10 August, and 27 September). On each sampling date, 3 random samples (i.e., exact sample locations were chosen randomly in the field by the sampler) from each of 3 riffle areas from above and below the waterfall barriers (6 riffles/stream) were collected from each study stream, for a total of 252 benthic samples over the study period. Samples could not be collected all year because of high flows in the late autumn and winter. However, the samples did encompass the primary period of production for the year, when light and temperature were at maximum levels. In addition, our study period extended through the major autumn runs of pink and chum salmon and into the period of carcass decomposition.

TABLE 1. List of taxa studied for secondary production. Taxa used were common in both study streams (Lessard and Merritt 2006). Chironomids were grouped at the family level for secondary production analyses. See Table 4 for more detailed taxonomic information on chironomids. Mayfly species are the dominant species observed in the 2 streams, but production was evaluated at the generic level for all mayflies. CPI = cohort production interval.

Order	Family	Genus	Species	CPI (mo)
Ephemeroptera	Baetidae	*Baetis*	*bicaudatus*	6
	Ephemerellidae	*Drunella*	*doddsi*	11
	Heptageniidae	*Epeorus*	spp.	11
		Cinygmula	spp.	11
		Rhithrogena	spp.	11
Diptera	Chironomidae			6

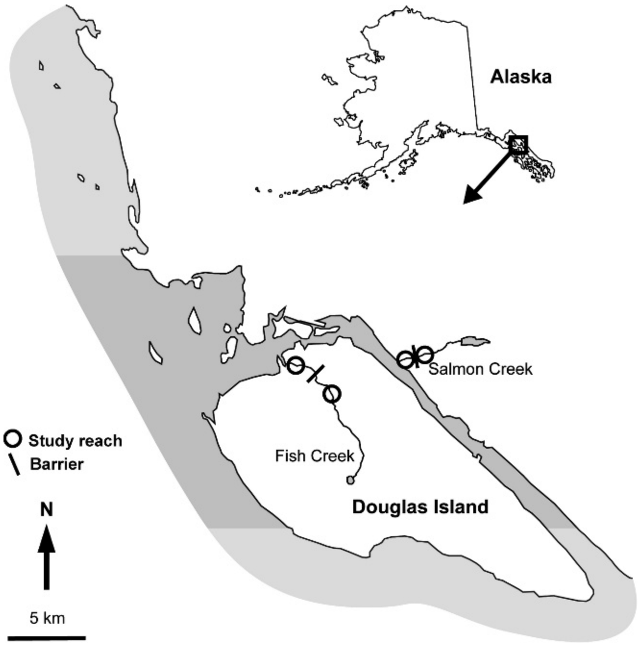

FIG. 1. Juneau–Douglas area of southeast Alaska and study stream locations. Barriers and study reaches are marked.

Samples were washed into labeled zip-top bags, fixed with 90% ethanol in the field, and transported back to the laboratory for processing. In the laboratory, samples were picked under magnification and sorted. Insects were identified to generic level using criteria from Merritt and Cummins (1996) and measured for total length. Biomass (dry mass) was calculated using length–mass regressions from Benke et al. (1999).

Secondary production rates of numerically dominant taxa were estimated with the size–frequency method (Benke and Huryn 1996). Production rates of mayflies were estimated for each genus, whereas production rates for chironomids were calculated at the family level. The latter approach might have produced inaccurate production estimates for chironomids, but the similarity between chironomid assemblages in upstream and spawning reaches within each stream allowed us to address relative differences in chironomid secondary production between upstream and spawning reaches. Cohort production intervals (CPIs) were estimated from size–frequency histograms of individual taxa and the literature (Minshall 1967, Radar and Ward 1987, Huryn 1990, DeWalt et al. 1994, Merritt and Cummins 1996, Huryn and Wallace 2000) (Table 1). Aquatic insect densities and CPIs can be highly variable and uncertain, and they strongly influence secondary production estimates. Therefore, a bootstrap procedure that incorporated minimum and maximum CPIs derived from field data was used to evaluate production estimates. One thousand randomly drawn samples with replacement were used to calculate 95% confidence intervals on final production estimates (Huryn 1996). Standing stock biomass means, standard errors, and statistical differences between stream reaches over the study period were calculated for each taxon using the

TABLE 2. Habitat data for upstream (control) and spawning reaches in Fish Creek and Salmon Creek, southeastern Alaska. Water temperature is shown as the range (mean) of mean daily temperatures. Width and depth are mean values.

Stream	Reach	Canopy	Substrate	Water temperature (°C)	Width (m)	Depth (cm)
Fish	Spawning	Conifer	Cobble/boulder	5–12 (7)	20.5	27.3
	Upstream	Conifer	Cobble/boulder	5–12 (7)	11.9	35.4
Salmon	Spawning	Conifer/alder	Cobble/boulder	4–10 (7.3)	11.4	26.6
	Upstream	Conifer	Cobble/boulder	4–10 (7.3)	9.7	30.9

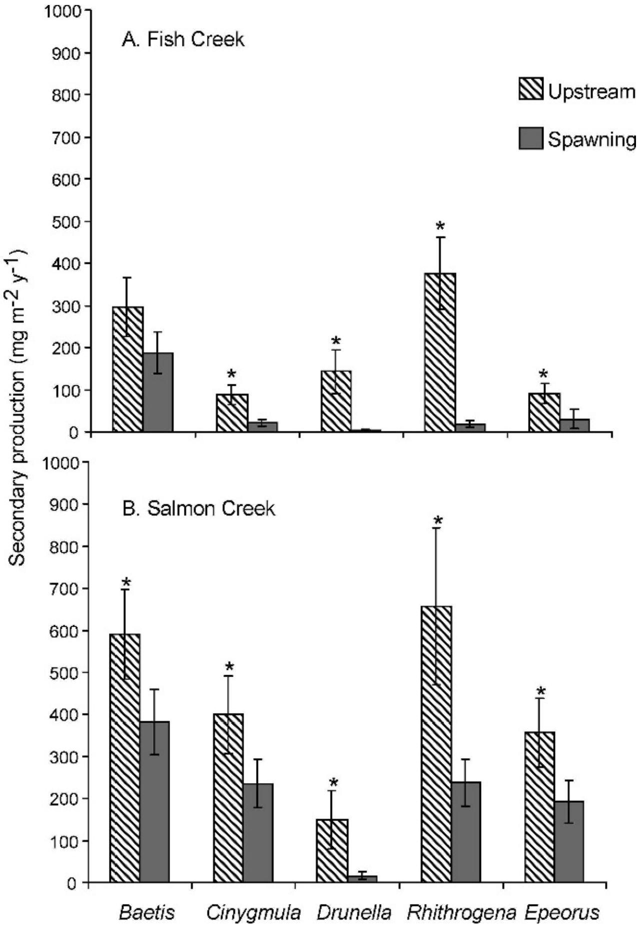

FIG. 2. Mean (±95% confidence interval [CI]) secondary production estimates of 5 mayfly genera in upstream (control) and spawning reaches of Fish Creek (A) and Salmon Creek (B). * denotes significant differences ($p \leq 0.05$) between spawning and control reaches in each stream.

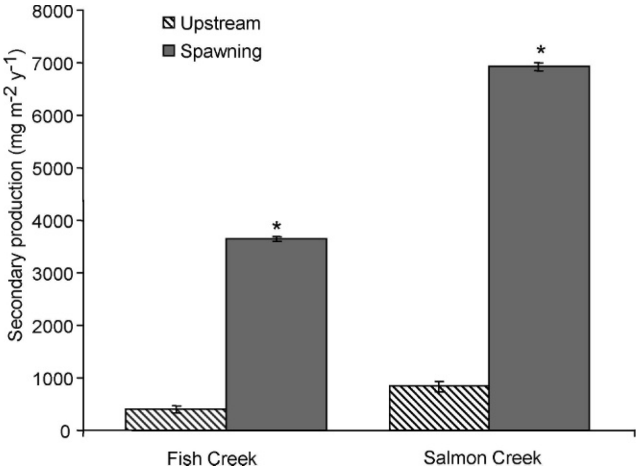

FIG. 3. Mean (±95% CI) secondary production of Chironomidae in upstream (control) and spawning reaches of Fish Creek (A) and Salmon Creek (B). * denotes significant differences ($p \leq 0.05$) between spawning and control reaches in each stream.

repeated measures analysis of variance (ANOVA) procedure in SYSTAT (SYSTAT for Windows, version 10.2; SYSTAT Software Inc., Richmond, California).

Results

Secondary production patterns of mayflies and chironomids were similar between study streams (Figs 2A, B, 3). All mayfly genera (*Baetis*, *Drunella*, *Cinygmula*, *Epeorus*, and *Rhithrogena*) had significantly higher secondary production in upstream than in spawning reaches (Fig. 2A, B), except that production of *Baetis* was significantly higher in the upstream reach only in Salmon Creek (Fig. 2B). Chironomid production showed the opposite pattern. Production rates of chironomids were >700% higher in spawning than in upstream reaches of both streams (Fig. 3). Differences in production between reaches represent differences in numbers of individuals and individual body size for each taxon (Table 3). Mayfly taxa generally were larger in upstream reaches, whereas chironomids were larger in spawning reaches.

Chironomid secondary production was analyzed at the family level, but the proportions of subfamilies and the number of dominant taxa were documented for each stream and stream reach (Table 4). Overall, the Orthocladiinae made up between 95% and 99% of the total chironomids in these streams, and Tanytarsini accounted for the remaining chironomids in both streams. Generic richness of chironomids was higher in upstream than in spawning reaches and, overall, was higher in Salmon Creek than in Fish Creek (Table 4).

Standing stock biomass varied across streams and taxa, but all taxa followed the general pattern of maximum biomass in the spring and summer followed by a sharp decline as autumn (and the salmon run) approached (Figs 4A–D, 5A–D, 6A, B). Both standing stock density and biomass were significantly higher in upstream reaches for mayflies and in spawning reaches for chironomids (repeated measures ANOVA; Table 5). Only *Baetis* biomass (Fig. 4D) did not differ between upstream and spawning reaches (Table 5). Biomass of all taxa reached minima during the spawning run, and mayflies were nearly eliminated from spawning reaches during the run (Figs 4A–D, 5A–D). Mayfly density also declined in upstream reaches after the run, but not as severely as in spawning reaches (Figs 4A–D, 5A–D). Chironomid biomass peaked just before the run in spawning reaches and then declined rapidly during the run (Fig. 5A, B). In late September,

TABLE 3. Mean (SE) density and biomass and maximum larval body lengths for mayfly genera and chironomids in spawning and upstream reaches in Fish Creek and Salmon Creek.

		Taxon					
Variable	Reach	*Baetis*	*Drunella*	*Rhithrogena*	*Epeorus*	*Cinygmula*	Chironomidae
Fish Creek							
Density (no./m^2)	Spawning	228.9 (43.7)	10.7 (2.4)	83.1 (44.3)	65.6 (20.6)	78.2 (41.1)	1966.8 (301.3)
	Upstream	686.7 (83.2)	37.4 (8.1)	193.5 (46.1)	128.1 (44.0)	136.9 (20.3)	278.6 (25.1)
Biomass (mg/m^2)	Spawning	35.4 (12.2)	0.5 (0.3)	7.4 (6.4)	4.5 (2.2)	4.0 (1.2)	157.8 (25.6)
	Upstream	48.4 (6.9)	32.3 (10.3)	66.4 (9.2)	13.6 (5.4)	14.9 (2.9)	19.4 (1.9)
Maximum length (mm)	Spawning	6.5	5	5	5.3	5.8	7
	Upstream	6	12.5	11	8	7	6
Salmon Creek							
Density (no./m^2)	Spawning	286.6 (125.0)	8.0 (3.4)	101.3 (26.9)	140.8 (54.3)	128.0 (45.2)	2403.9 (337.8)
	Upstream	423.6 (74.6)	25.3 (6.1)	178.3 (20.1)	266.1 (74.0)	182.3 (36.4)	658.0 (77.3)
Biomass (mg/m^2)	Spawning	67.5 (29.2)	8.1 (6.2)	38.7 (9.4)	69.6 (8.1)	45.2 (15.4)	161.1 (18.9)
	Upstream	113.8 (28.9)	69.6 (29.6)	121.6 (26.5)	28.7 (19.4)	80.3 (18.6)	41.7 (4.1)
Maximum length (mm)	Spawning	8.5	11.5	9	7.5	7.5	12
	Upstream	6.5	13.5	11	7.5	7.5	6

TABLE 4. Common genera and the proportion of chironomid subfamilies or tribes in spawning and upstream (control) reaches of Fish Creek and Salmon Creek.

Stream	Reach	Subfamily/tribe	Proportion	Common genera
Fish Creek	Spawning	Orthocladiinae	96.3	*Corynoneura* *Crictopus* *Eukiefferiella* *Orthocladius*
		Tanytarsini	3.7	*Microspectra*
	Upstream	Orthocladiinae	99.3	*Corynoneura* *Eukiefferiella* *Orthocladius* *Paraphaenocladius* *Tvetenia*
		Tanytarsini	0.7	*Zavrelia*
Salmon Creek	Spawning	Orthocladiinae	96.6	*Brillia* *Corynoneura* *Eukiefferiella* *Orthocladius* *Thienemanniella* *Tvetenia*
		Tanytarsini	3.5	*Cladotanytarsus*
	Upstream	Orthocladiinae	90.6	*Corynoneura* *Eukiefferiella* *O. (Euorthocladius)* *Orthocladius* *Paraphaenocladius* *Paratrissocladius* *Psectrocladius* *Thienemanniella* *Tvetenia*
		Tanytarsini	9.4	*Microspectra* *Tanytarsus*

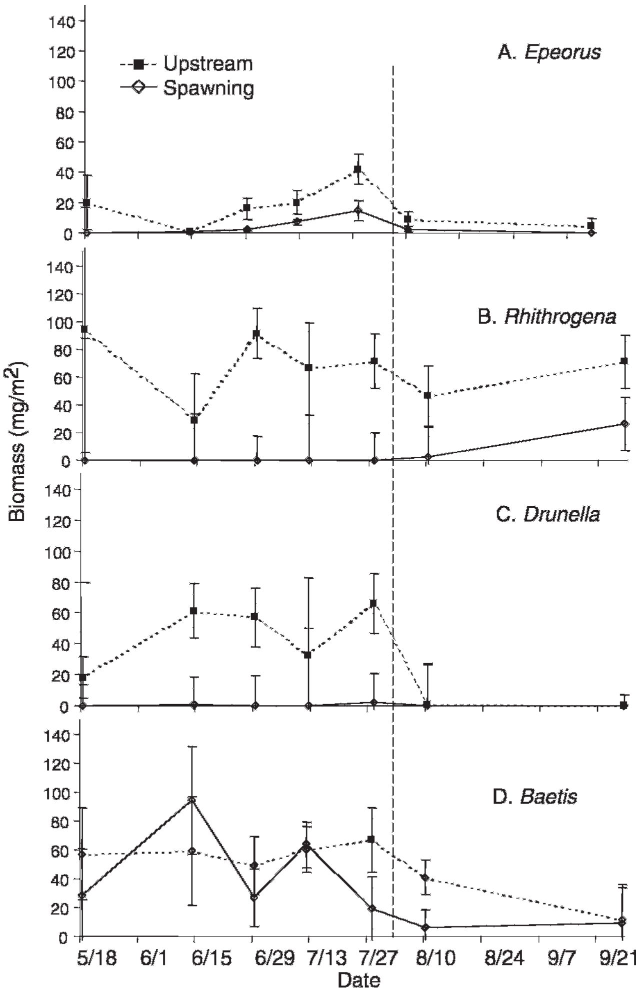

FIG. 4. Mean (±1 SE) standing stock biomass of mayfly genera across sampling dates in upstream and spawning reaches of Fish Creek. The vertical dotted line represents the approximate start of the spawning run. Dates are formatted as day/month in 2002.

after the run and once carcass decomposition was well underway in the spawning reaches, biomass differences between reaches showed the same pattern as before the run, with mayflies remaining higher upstream and chironomids higher in spawning reaches.

Discussion

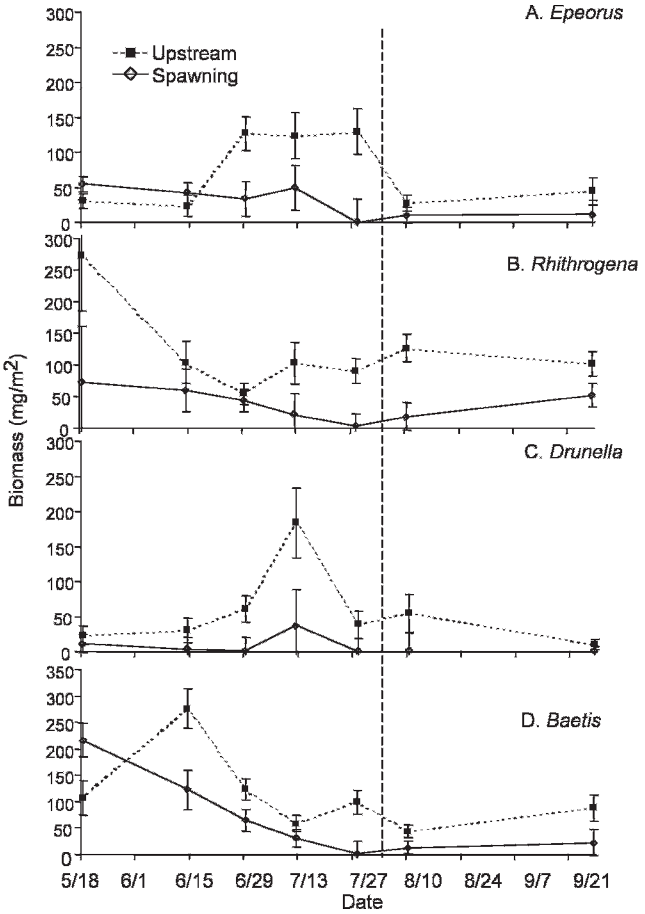

FIG. 5. Mean (±1 SE) standing stock biomass of mayfly genera across sampling dates in upstream and spawning reaches of Salmon Creek. The vertical dotted line represents the approximate start of the spawning run. Dates are formatted as day/month in 2002.

Theories on the linkages between nutrients from spawning salmon and juvenile salmonid production include many intermediate steps as nutrients flow through stream communities via bottom-up processes to juvenile salmonids (Kline et al. 1997, Lichatowich 1999, Gende et al. 2002). These theories have been bolstered by use of stable isotopes to trace MDN into stream biofilm, aquatic insects, and resident fish (Bilby et al. 1996, Chaloner et al. 2002a, Claeson et al. 2006, Honea and Gara 2008). Studies comparing standing stock of selected taxa in both natural and artificial streams have found differences that also implied a nutrient subsidy effect of MDN (Kline et al. 1997, Wipfli et al. 1998, 1999). However, incorporation of MDN into stream communities and short-term increases in aquatic insect standing stock biomass in salmon spawning reaches do not necessarily mean that these nutrient inputs lead to increases in aquatic insect secondary production. Spawning runs cause a large disturbance of the stream benthos before MDN enrichment occurs (Minakawa 1997, Peterson and Foote 2000, Honea and Gara 2008, Moore and Schindler 2008, Monaghan and Milner 2009). The level of disturbance increases with the number of spawners (Moore and Schindler 2008), so that disturbance effects increase with enrichment potential. This relationship is particularly true of the pink-

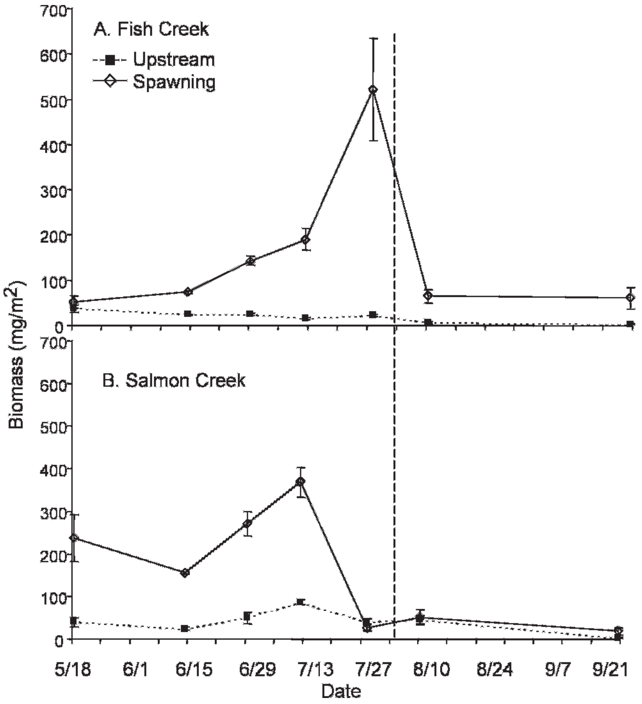

FIG. 6. Mean (±1 SE) standing stock biomass of Chironomidae across sampling dates in upstream and spawning reaches of Fish Creek (A) and Salmon Creek (B). The vertical dotted line represents the approximate start of the spawning run. Dates are formatted as day/month in 2002.

and chum-dominated runs of southeastern Alaska, where it is common for thousands of fish to rush into small (1^{st}–3^{rd} order) coastal streams and disturb sediments with their density, displays of territoriality, and nest digging (Honea and Gara 2008, Tiegs et al. 2008, Monaghan and Milner 2009). For enrichment mechanisms of MDN to be understood in natural stream systems, the physical act of spawning must precede the enrichment, something that cannot be accomplished in mesocosm studies. Similarly, pre- and postspawning standing stock studies of insect abundance and biomass proximate to the autumn salmon runs do not provide information about processes operating during the primary growing season in these streams. The results of short-term standing stock studies are especially difficult to interpret because benthic insects are locally attracted to carcasses in streams (Minakawa 1997, Chaloner et al. 2002b). Thus, local increases in abundance can be mistaken for systemwide increases in benthic production. Our study is the first to document differences in aquatic insect secondary production in relation to natural MDN enrichment.

Our study revealed several interesting patterns that call into question the current paradigm on the relationship between salmon and energy flow in streams. For relatively large univoltine taxa, such as ephemerellid and heptageniid mayflies, secondary production was consistently higher in upstream reaches where salmon were blocked from spawning than in spawning reaches. One possible explanation for this pattern is that high mortality of these taxa caused by spawning disturbance eclipses the potential enrichment effects of salmon. Upstream reaches might be areas of refuge that allow greater production than in spawning reaches. This supposition is supported by the observation that mean biomass of these mayflies was higher in upstream than in spawning reaches in spring, months after the last salmon run. Species of univoltine mayflies that have an overwintering cohort (e.g., *Rhithrogena* spp.) were severely reduced in spawning reaches by the

TABLE 5. Results (*p*-values, *F*-ratio) of repeated measures analysis of variance used to compare standing stock density and biomass for mayfly genera and chironomids between upstream and spawning reaches of the 2 study streams. Nonsignificant *p*-values (>0.05) are in bold. Degrees of freedom = 1 for all comparisons.

		Density		Biomass	
Stream	Taxon	*p*-values	*F*	*p*-values	*F*
Fish Creek	*Baetis*	0.011	16.710	**0.279**	1.257
	Cinygmula	0.023	6.358	0.003	12.479
	Drunella	0.000	34.752	0.002	13.503
	Epeorus	0.000	20.615	0.000	28.739
	Rhitrogena	0.000	68.095	0.000	33.164
	Chironomidae	0.000	67.136	0.000	65.427
Salmon Creek	*Baetis*	0.023	6.368	0.016	7.210
	Cinygmula	0.032	5.518	0.006	10.035
	Drunella	0.002	14.529	0.000	19.291
	Epeorus	0.001	16.198	0.011	8.273
	Rhitrogena	0.028	5.867	0.008	9.016
	Chironomidae	0.000	257.753	0.000	323.850

autumn salmon runs. Further support for the negative influence of salmon disturbance on large-bodied mayflies comes from the finding that, in May, large individuals of *Drunella* spp. and *Rhithrogena* spp. were found in upstream reaches, whereas only small individuals were found in spawning reaches (JLL, unpublished data). Moreover, mayfly life histories do not appear to be timed to benefit from the autumn pulse of MDN in these streams. Mayfly biomass declined in both reaches in both streams in the autumn just before the salmon run, but the declines were most pronounced in the spawning reaches. This pattern might be a consequence of an historical legacy in which disturbance impacts from salmon over thousands of years have favored emergence just before the salmon run, a hypothesis also suggested by others (Moore and Schindler 2008). However, in Alaska, the autumn spawning period also coincides with increasing rains and spates that add to the inhospitable environment for large-bodied insects in these streams (Lytle 2002).

The response of chironomids in these streams followed the predictions of the MDN enrichment theory. Secondary production of chironomids was consistently much higher in spawning than in upstream reaches. The major production period for chironomids occurred during the spring and summer. Like the mayflies, chironomid biomass declined during the run and remained low well into the carcass decomposition period. Unlike the mayflies, chironomid standing stock biomass peaked just before the autumn spawning run in spawning reaches but remained steady in upstream reaches. Several factors could have influenced the patterns observed for chironomids, but the focus of our research did not allow us to test all possible mechanisms.

Chironomids might be able to avoid high mortality from spawning disturbance if their small size allows them to take advantage of hyporheic or interstitial spaces. This ability would allow chironomids to maintain higher population levels than larger-bodied taxa, such as mayflies, in spawning reaches. However, this mechanism does not explain why chironomid production was low in upstream reaches throughout the growing season. The high production of mayflies in upstream reaches indicates that food resources probably were not limiting. The lack of mayflies in spawning reaches might have led to decreased invertebrate competitive or predatory interactions (*Drunella* are considered predators at larger sizes), so that chironomids were able to grow at higher rates in spawning than in upstream reaches. However, other studies have shown that salmon spawning increases drift and fish predation on insects, primarily chironomids (Peterson and Foote 2000).

In our study, chironomid standing stock biomass in spawning reaches peaked before the run and declined sharply during the run. In Salmon Creek, chironomid biomass decreased sharply downstream right before the run began, a pattern that suggests an emergence might have occurred. Emergence of chironomids before the peak run of salmon would allow these short-lived, multivoltine taxa to avoid the large disturbance of spawning and to produce a cohort able to capitalize on the carcass-decomposition period. Adult carcasses in all stages of decomposition can be seen littering the stream bottoms and collecting in pools in these streams 4 to 6 wk after the major runs begin (JLL, unpublished data). Honea and Gara (2008) found that marine-derived N and C in aquatic macroinvertebrate biomass were maximized in a spawning reach in Washington 3 mo after spawning. Even if the decrease in chironomid biomass in our spawning reaches was caused by spawning-related mortality, standing stock biomass of chironomids in spawning reaches was nearly equal to that of all mayflies combined in the postrun period. The remaining individuals and any cohorts that arrived after the run could capitalize on the MDN enrichment.

Fish community structure differed between upstream and spawning reaches. Sculpin (*Cottus* sp.), resident and ocean-run Dolly Varden (*Salvelinus malma malma*), and juvenile salmonids occurred in spawning reaches, but only Dolly Varden occurred in upstream reaches (J. Hudson, US Forest Service, personal communication). The direct and indirect effects of spawning in conjunction with associated predation by juvenile salmonids and other species on benthic insects are probably important mechanisms for insect community dynamics in these streams. The benefits of positive indirect effects of predatory fish on chironomids (via direct negative effects on their competitors and predators) can outweigh the direct negative effects of fish predation on chironomids (Power et al. 1992, Batzer et al. 2000, Rosenfeld 2000). Therefore, spawning disturbance, fish predation, and biotic interactions between benthic insects probably interacted to create the benthic community production patterns observed in our study.

Chironomids are primary colonizers of salmon carcasses during decomposition (Chaloner et al. 2002b), so the chironomid community might have been temporarily diverted to the carcasses from other areas in the stream with the result that densities on mineral substrates were reduced during the carcass-decomposition period. This explanation could not be confirmed because we did not sample carcasses. However, in Salmon Creek, chironomid biomass decreased before the run began, so a change in numbers of chironomids in the stream seems to be a more likely explanation than a change in distribution for the observed reductions in standing stock biomass. A net effect of the ability of chironomids to capitalize on MDN during carcass decomposition before winter should have been increased production of overwintering cohorts in spawning reaches. In spring, chironomid density and biomass were higher in spawning than in upstream reaches of both streams.

Differences in the patterns of mayfly and chironomid production might have been caused by disturbance-related differences in food resources between spawning and upstream reaches. Functional feeding group composition provides evidence in support of this mechanism. Spawning disturbs the sediments, so autumn periphyton communities should have been less variable in undisturbed upstream reaches than in spawning reaches, and scrapers should have been more successful in stable upstream reaches than in disturbed spawning reaches. We found that ephemerellids and heptageniids were more abundant in upstream than in spawning reaches. Decomposing salmon particles are abundant in spawning reaches during the light-limited autumn–winter period. The combination of unconsolidated sediments and high-quality fine particulate organic matter (FPOM) should have benefited collector–gatherers (e.g., some chironomid taxa) in the spawning reaches relative to the control reaches. We found that chironomids of the subfamily Orthocladiinae were the dominant chironomid group in spawning reaches in both study streams. In contrast, facultative collector–gatherers, such as baetid mayflies, should have thrived in both upstream and spawning reaches. We found that secondary production of baetids differed less between spawning and upstream reaches than did secondary production of all other mayfly genera.

Thus, our results suggest that spawning disturbance is a major driving force organizing benthic communities in southeastern Alaska streams. They also suggest that high secondary production of mayflies in upstream reaches might impose biotic constraints on chironomid communities in upstream reaches. We hypothesize that production limits are reversed in reaches open to the ocean because of the cycle of salmon spawning disturbance, predatory fish diversity (resident species, juvenile salmonids, and oceanic transient species), and MDN inputs, which interact to favor chironomid production in spawning reaches. It is not clear whether salmon affect chironomids indirectly by limiting invertebrate competitors and predators or stimulate chironomid production directly via nutrients provided by spawners. It also is not clear whether lower mayfly secondary production in spawning than in upstream reaches was caused by greater fish predation in spawning reaches or by the spawning disturbance. Honea and Gara (2008) suggested that fish predators in spawning reaches might consume increased macroinvertebrate production and obscure our ability to detect MDN-stimulated secondary production. These mechanisms probably act simultaneously to generate the production patterns observed in our study. Therefore, the link between MDN and juvenile salmonid production in these systems might consist solely of chironomid production. Both pink and chum salmon feed mainly on chironomids during their seaward migration (Frolenko 1973, Loftus and Lenon 1977, Kaeriyama et al. 1978). Chinook and coho juveniles also feed predominantly on chironomids (Loftus and Lenon 1977, Dauble et al. 1980). We showed that responses of secondary production to MDN varied among taxa in southeastern Alaskan streams. In these streams, the linkages between anadromy and juvenile salmon production might have less to do with systemwide stream enrichment than with enrichment of individual taxa or groups of taxa. Interactions among spawning disturbance, macroinvertebrate life histories, and stream community structure in spawning streams require further study so that variation in responses to salmon nutrients can be better understood and incorporated into MDN theory.

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