

Biotic disturbance and benthic community dynamics in salmon-bearing streams

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Summary

1. Organisms can impact ecosystems via multiple pathways, often with positive and negative impacts on inhabitants. Understanding the context dependency of these types of impacts remains challenging. For example, organisms may perform different functions at different densities.

2. Anadromous salmon accumulate > 99% of their lifetime growth in marine ecosystems, and then return to spawn, often at high densities, in relatively confined freshwaters. While previous research has focused on how salmon nutrients can fertilize benthic communities, we examined how an ecosystem engineer, sockeye salmon *Oncorhynchus nerka*, influences seasonal dynamics of stream benthic communities through their nest-digging activities in south-western Alaska, USA. Benthic invertebrate and algal abundance were quantified every 7–14 days during the open water seasons of 10 streams in riffle and run habitats across multiple years, leading to 25 different stream-year combinations that spanned a large gradient of salmon density.

3. In streams with few or no salmon, benthic algal and insect biomass were fairly constant throughout the season. However, in streams with more than 0.1 salmon m⁻², algal and insect biomass decreased by an average of 75–85% during salmon spawning. Algal biomass recovered quickly following salmon disturbance, occasionally reaching pre-salmon biomass. In contrast, in streams with more than 0.1 salmon m⁻², aquatic insect populations did not recover to pre-salmon levels within the same season. We observed no positive impacts of salmon on algae or insects via fertilization from carcass nutrients.

4. Salmon, when their populations exceed thresholds in spawning density, are an important component of stream disturbance regimes and influence seasonal dynamics of benthic communities. Human activities that drive salmon densities below threshold densities, as has likely happened in many streams, will lead to altered seasonal dynamics of stream communities. Human activities that alter animal populations that are sources of biogenic disturbance can result in shifts in community dynamics.

Key-words: bioturbation, ecosystem engineer, marine-derived nutrients, *Oncorhynchus nerka*, succession.

Introduction

Organisms can impact ecosystems via multiple pathways, often with positive and negative impacts on coinhabitants. For example, many plants act as competitors under some circumstances or scales, even while acting as facilitators under other conditions (Callaway & Walker 1997). Alternatively, *Prochilodus*, a dominant detritivorous fish, has been found to alter tropical stream ecosystems via several pathways. Large- and small-scale experiments have demonstrated that through foraging on detritus and perturbing benthic habitats, *Prochilodus* decrease sediment accrual rates and periphyton abun-

dance (Flecker 1997), decreasing primary productivity and altering carbon cycling (Taylor, Flecker & Hall 2006). However, McIntyre *et al.* (2007) predicted that these fish could positively impact primary producers by excreting large amounts of limiting nutrients. Reconciling the different pathways by which organisms alter their ecosystems under different contexts is particularly challenging given the increasing realization that organisms can exert large impacts via both trophic (e.g. predation) and nontrophic interactions (e.g. ecosystem engineering) (Bruno, Stachowicz & Bertness 2003; Wright & Jones 2006).

One aspect of context dependency is the functional relationship between the density of a species and its impact on its environment. For example, the relationships between densities of bioturbators, a type of ecosystem engineer, and their impacts

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on aquatic ecosystems are relatively understudied (Moore 2006). Understanding these relationships is increasingly important in light of concerns regarding the ecological consequences of declines in biomass of benthic bioturbators due to anthropogenic impacts (e.g. Coleman & Williams 2002; Taylor *et al.* 2006). While a recent simulation analysis assumed that impacts of bioturbators increase linearly with population density (Solan *et al.* 2004), it seems likely that impacts of these organisms may often be a nonlinear function of population densities. For example, Flecker, Feifarek & Taylor (1999) found a saturating relationship between tadpole density and sediment accumulation – at five tadpoles per square metre, sediment accumulation ceased decreasing as a function of increasing tadpole density. Identifying these relationships will aid understanding when organisms contribute substantially to disturbance regimes, and subsequently understanding how human activities may change disturbance regimes.

Pacific salmon *Oncorhynchus* spp. may exert strong impacts on coastal stream communities via several pathways. Anadromous and semelparous salmon accumulate over 99% of their mass during the ocean phase of their life history, and then return to coastal freshwaters to spawn and die (Quinn 2005). Through foraging in the productive and vast oceanic ecosystem, salmon can reach large sizes and spawn at high densities relative to the confined coastal freshwaters in which they spawn. Salmon dig large nests during spawning, perturbing benthic habitats of spawning reaches (Montgomery *et al.* 1996; Gottesfeld *et al.* 2004). Indeed, an experimental exclusion of salmon suggested that salmon nest digging decreases fine sediment accumulation and algal biomass (Moore, Schindler & Scheuerell 2004). In addition, several studies have observed decreases in algal and benthic insect biomass during salmon spawning in a single or a few local areas (e.g. Hildebrand 1971; Field-Dodgson 1987; Peterson & Foote 2000; Minakawa & Gara 2003; Lessard & Merritt 2006). While these studies have documented substantial local impacts of salmon nest digging on streams, the relationship between salmon population density and their impact on benthic communities remains unknown. In addition, previous research on the impacts of salmon on streams has emphasized how nutrients from salmon carcasses, derived from oceanic ecosystems due to their anadromous life history, may subsidize streams from the bottom-up (*sensu* Polis, Anderson & Holt 1997; reviewed by Gende *et al.* 2002; Naiman *et al.* 2002). Specifically, experimental additions of salmon carcasses have suggested that nutrients from salmon can fertilize stream food webs, increasing algal and benthic invertebrate biomass (e.g. Wipfli, Hudson & Caouette 1998; Chaloner & Wipfli 2002) and comparative studies have observed increased nutrients and algae in response to spawning salmon (e.g. Johnston *et al.* 2004). Thus, it is unknown whether salmon have net positive (fertilization via salmon-derived nutrients) or net negative (disturbance from nest-digging) impacts on stream benthic communities, and how or if these roles change as a function of salmon density.

The objective of this study was to examine how different densities of salmon alter the seasonal dynamics of stream benthic communities. By quantifying the seasonal dynamics

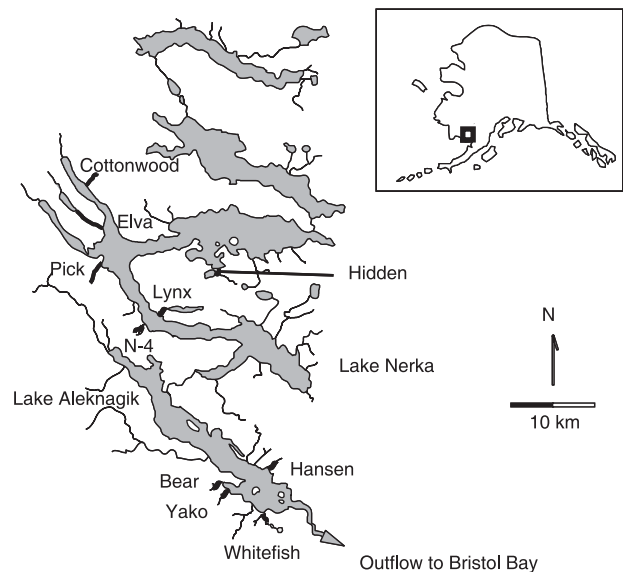


Fig. 1. Map of study locations, in the Wood River system of the Bristol Bay region of south-eastern Alaska. Streams are highlighted by bold. Inset demonstrates the location of this system in the state of Alaska, USA.

of benthic algae and invertebrates in at least 25 stream-year combinations, we show for the first time that above a threshold density of salmon, bioturbation by nest-digging salmon consistently causes drastic decreases in algal and insect biomass. We did not observe any fertilization impacts of salmon on benthic communities at any densities. This study demonstrates that salmon are an important component of stream disturbance regimes, and that population declines of salmon likely change the fundamental disturbance regimes characteristic of coastal stream ecosystems.

Methods

STUDY SITE

This study was based on streams in the Wood River system of south-western Alaska, USA. This 300 000 ha river system is a spawning and nursery habitat for anadromous sockeye salmon (*O. nerka*). An average of 1.1 million sockeye spawn in the creeks, rivers and beaches of this system every year. An additional 1.8 million sockeye on average are harvested every year prior to spawning (Baker *et al.* 2006). We quantified how salmon altered seasonal dynamics of stream benthic communities for up to five summers on 10 streams for a total of 25 and 27 stream-year combinations for benthic invertebrate and periphyton, respectively (Table 1; Fig. 1). Streams spanned a natural gradient in salmon densities (0–0.54 salmon m⁻²). This gradient in salmon densities was achieved through year to year variation in salmon returns and differences in densities among streams (Table 1). A previous survey of our study streams found that much of their total habitat was suitable for salmon spawning (Marriott 1964). Based on this survey, spawning habitat comprised the following proportions of total stream areas: Bear = 0.85, Elva = 0.15, Hansen = 1.0, Hidden = 0.87, Lynx = 0.6, Pick = 0.9,

Table 1. Streams and years sampled for the seasonal dynamics of benthic communities. Unless otherwise noted, both benthic invertebrates and algal dynamics were quantified for these stream-years. Salmon density represents the maximum observed live salmon density. Flow data represent the maximum and minimum observed flows and the dates of those observations for each stream-year and are from Moore *et al.* (2007)

Stream	Year	Salmon m ⁻²	Flow [m ³ s ⁻¹ (date)]	
			Minimum	Maximum
Bear	2004*	0.20	0.12 (8/20)	0.60 (6/17)
	2005†	0.25	0.09 (8/02)	1.01 (8/24)
Cottonwood	2002	0.00	0.02 (9/03)	1.18 (6/23)
	2003	0.00	0.10 (8/05)	3.17 (6/26)
	2004	0.00	0.0 (8/04)	1.86 (6/27)
	2005	0.01	0.04 (8/16)	0.74 (6/21)
Elva	2002	0.05	0.64 (9/03)	3.15 (6/23)
	2005	0.15	1.02 (8/16)	8.81 (6/21)
Hansen	2004*	0.04	0.05 (7/25)	0.13 (6/16)
	2005†	0.02	0.03 (8/09)	0.09 (6/15)
Hidden	2001	0.12	NA	NA
	2002	0.13	0.13 (9/03)	0.64 (6/25)
	2003	0.27	0.16 (8/05)	0.77 (6/21)
	2004	0.20	0.29 (8/18)	0.59 (6/25)
	2005	0.19	0.14 (8/16)	0.71 (6/21)
Lynx	2002	0.06	0.31 (8/06)	1.03 (6/22)
	2003	0.07	0.37 (7/21)	2.48 (8/23)
	2004	0.54	0.31 (9/08)	1.20 (6/12)
	2005	0.25	0.17 (8/14)	1.41 (6/16)
N-4	2003	0.00	0.05 (8/06)	0.09 (6/26)
	2004	0.16	0.06 (7/24)	0.10 (6/12)
	2005	0.00	0.04 (7/19)	0.08 (9/23)
Pick	2001	0.16	NA	NA
	2002	0.14	0.26 (9/06)	1.14 (6/24)
	2003	0.16	0.28 (7/27)	1.41 (8/21)
	2004	0.33	0.24 (7/24)	1.18 (6/11)
	2005	0.30	0.44 (8/12)	1.49 (6/16)
Whitefish	2004*	0.01	0.18 (8/09)	0.57 (6/16)
	2005†	0.06	0.16 (8/15)	0.37 (6/25)
Yako	2004*	0.36	0.20 (7/20)	0.48 (6/16)
	2005†	0.25	0.10 (8/09)	0.61 (6/15)

NA, cases where data are not available.

*Only benthic invertebrates, not algae, were quantified this stream-year.

†Only algae, not benthic invertebrates, were quantified this stream-year.

Whitefish = 0.75, Yako = 0.5; note that Cottonwood and N-4 were not surveyed in this study. Across all of our study streams, salmon were almost exclusively sockeye (> 98% of total counted salmon). Water flows generally were highest in the early spring associated with snowmelt or in the late summer associated with fall rainstorms (Table 1). Flows tended to be lowest during July and early August, the period of peak salmon spawning. We monitored benthic communities every 11.3 ± 4.3 days (mean ± 1 SD) from June up until late August or September in 2001–05. This seasonal period spanned the bulk of the ice-free period, and included times before, during and after salmon spawning. At each sampling period we estimated salmon densities in each stream by visually enumerating salmon and dividing these counts by the wetted channel area. These salmon density estimates were performed on the stretch of stream between the mouth of the stream and the uppermost sampling location located

near the upstream extent of salmon spawning in each stream. Maximum observed live salmon densities for each stream-year were used as an index of salmon abundance.

PERIPHYTE

During each sampling period we quantified periphyton biomass (chlorophyll-*a* cm⁻²) on naturally occurring rocks in our study streams. On average we quantified algae on 5.3 ± 0.9 rocks (± 1 SD) per stream per sampling date. Each rock was collected haphazardly from a different sampling location. Sampling locations were selected to maximize coverage of the length of the stream accessible to salmon, were located in runs, and were held constant throughout the length of the study. We sampled rocks that were small cobble (maximum surface area was 252 cm²). Rocks were scrubbed with a small brush, and vigorously rinsed to remove all benthic algae. We filtered a known fraction of the filtrate through 47 mm GF/F silica filters (pore size = 0.7 µm). The filters were frozen at -10 °C and later solubilized in methanol. Subsequently, we determined the concentrations of chlorophyll-*a* with fluorimetry (Steinman, Lamberti & Leavitt 2006). To calculate the amount of chlorophyll-*a* on an areal basis (µg cm⁻²), we estimated the surface area of each collected rock by assuming it was a rectangular box and measuring its average length, width and height. The average rock was 102.8 ± 38.8 cm² (± 1 SD; *n* = 1186).

BENTHIC INVERTEBRATES

Benthic invertebrate communities were also quantified during the open water seasons of streams, concurrent with periphyton sampling. At each sampling event we collected 4.8 ± 1.3 Surber samples (± 1 SD; 0.5-mm mesh; sampling to a depth of 10 cm; *n* = 1063), each from a different sampling location in the stream (see above for description of sampling locations). Samples were preserved in 70% ethanol. Invertebrates were sorted and identified to the taxonomic resolution listed below (Merritt & Cummins 1996; Stewart & Stark 2002; Adams 2004). For each taxa in each sample, the body length of five to 10 random individuals was measured using an ocular micrometer. Body lengths were converted to dry masses using taxon specific length–mass relationships determined for these streams (J.W. Moore, unpublished data). Total dry mass of each taxonomic group in each sample was estimated by multiplying abundance by the average mass of an individual in that sample. For the purposes of this study, we combined invertebrate taxa into the following five categories corresponding to order or higher: Ephemeroptera (primarily Heptageniidae, Baetidae and Ephemerellidae), Plecopterans (primarily Chloroperlidae, Nemouridae and Perlolidae), Tricopterans (primarily Brachycentridae and Limnephilidae), Dipterans (primarily Chironomidae, Tipulidae, Simuliidae and Ceropogonidae) and other (primarily Turbellaria, Acarina and Oligochaeta).

STATISTICAL ANALYSES

All statistical analyses were performed using SYSTAT 11.0. For most analyses on algae and invertebrate dynamics, we used each stream-year as the unit of replication. The possibility that average spring algal biomass is influenced by salmon abundance the previous year was statistically examined using a General Linear Model (GLM) with salmon density in the previous year and stream as potential factors. For this analysis, average spring algal biomass was cube root transformed to improve normality. On a finer time-scale, a

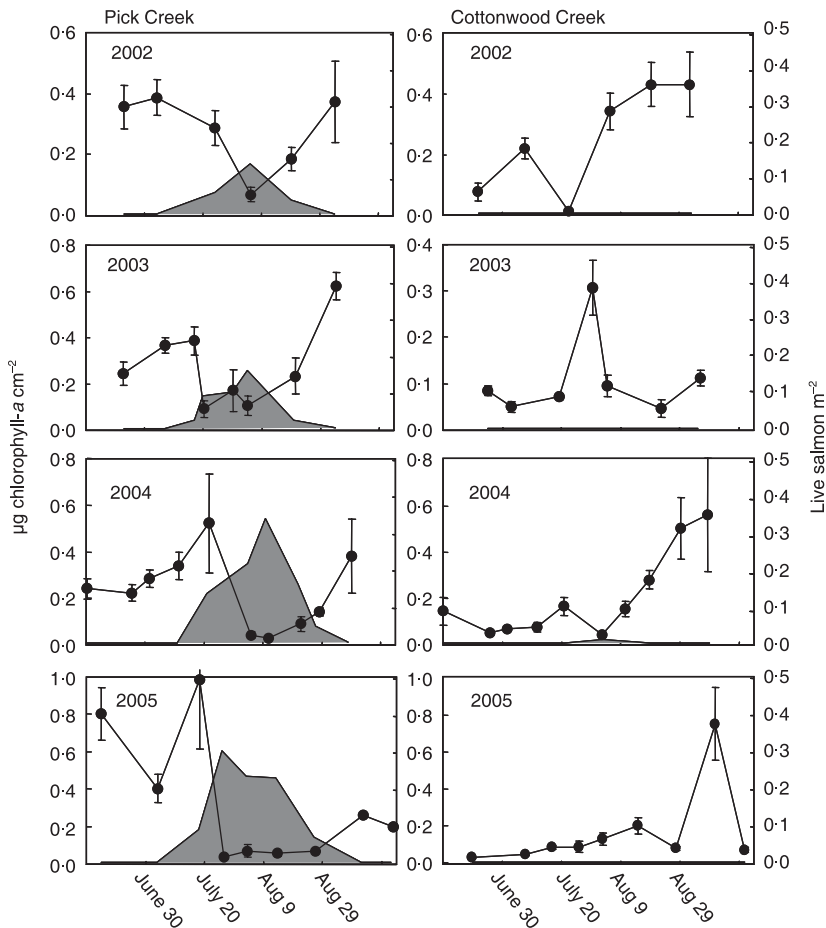


Fig. 2. Seasonal dynamics of algal biomass in a representative stream with, and without, high densities of salmon, across years. Filled circles with error bars represent the mean \pm 1 standard error of the mean (SEM) of algal biomass, as quantified by chlorophyll-*a*. Salmon densities are represented by shaded areas that correspond to the right y-axis. Note the different scales on the left y-axis.

regression was run to investigate how salmon density impacted average algal biomass for a given date. For this analysis, algal data was \ln -transformed to improve normality. In addition, for each stream-year, we estimated the proportional change in algal and invertebrate biomass from the spring to salmon spawning period. Proportional change was calculated as the proportional difference between average spring algal biomass and algal biomass during maximum salmon density. For streams without salmon, the period corresponding to maximum salmon densities occurred at the beginning of August. We fit a power function to the relationship between spawner density and the seasonal change in algal biomass. The same function was used to fit relationships between spawner densities and seasonal changes in biomass of invertebrate taxa. In addition, to explicitly compare across taxa, we investigated how invertebrate biomass changed through the season by comparing proportional change in stream-years with low salmon densities (< 0.1 salmon m^{-2}) to stream-years with high salmon densities. This threshold was chosen based on data inspection. We then ran a two-factor ANOVA with taxa and salmon density (high vs. low) as potential effects. This ANOVA was run once for each taxa, considering each stream-year to be a replicate. Caddisflies were excluded from these analyses because they were often at low densities, rendering poor estimates of changes in proportional change. Following a significant result, we ran post-hoc paired *t*-tests to examine how different taxa responded differently to salmon with an adjusted α for multiple comparisons.

Results

IMPACTS OF SALMON ON PERIPHYTON

Salmon nest-digging strongly impacted algal dynamics in streams with high densities of salmon. Specifically, algal biomass tended to increase through the spring, but then decrease as salmon entered streams and initiated spawning (Fig. 2). For example, in Pick Creek in 2004, algal biomass increased through the spring, but then decreased 94% when salmon first entered the stream. Throughout the salmon spawning period that lasted approximately a month, algal biomass was maintained at low levels. When all salmon in Pick Creek died, algal biomass rebounded to pre-salmon levels. In contrast, in streams with low densities of salmon, algal biomass tended to increase through the year, although there was some stochasticity, perhaps due to flow regime (see Fig. 2). For example, in Cottonwood, the temporary drop in algal biomass was associated with a period of extremely low flows (Table 1). In years and streams with low or no spawning salmon (< 0.1 salmon m^{-2}), algal biomass tended to increase 20% (± 33.3 ; ± 1 SEM), although there was substantial variability in the seasonal progression in algal biomass (Fig. 3). Above this threshold density, algal biomass decreased 74% on average (± 5.5 ; ± 1 SEM) (Fig. 3). In fact,

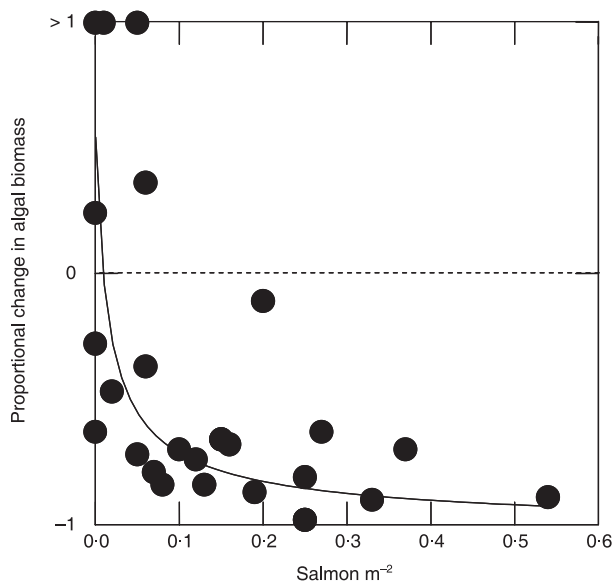


Fig. 3. Summary of the seasonal changes in algal biomass as a function of salmon density. Each point represents the proportional change in algal biomass of a given stream-year, as a function of the observed maximum live salmon density of that stream-year. Proportional change was calculated as the proportional difference between average spring algal biomass and algal biomass during maximum salmon density. The dotted line through 0 represents stream-years with no change, below this line indicates a decrease, and above this line represents a stream-year with increased algal biomass. For streams without salmon, the period corresponding to maximum salmon densities occurred at the beginning of August. The line shown represents the best fit of a power function ($r^2 = 0.41$). Salmon density represents the maximum observed live salmon density in the study stream during that year. Note that the y -axis cut-off several data points that were subsequently located at $y > 1.0$.

algal biomass decreased in every stream and year with salmon densities above $0.06 \text{ salmon m}^{-2}$.

There was no evidence that salmon increased algal biomass via fertilization by carcass nutrients. While individual streams had significantly different average spring chlorophyll-*a* biomass (GLM, stream effect: $F_9 = 5.93$; $P = 0.002$), the spawning density of salmon the previous year in that stream had no significant impact on average spring algal biomass (GLM, salmon density effect: $F_1 = 1.572$, $P = 0.22$). On a finer time-scale, salmon density at the time of sampling was in fact significantly negatively related to algal biomass of that date across all sampling events and streams (regression between salmon and algal biomass: $r^2 = 0.08$, $P < 0.001$).

IMPACTS OF SALMON ON BENTHIC INVERTEBRATES

Salmon nest-digging also strongly influenced the seasonal dynamics of benthic invertebrates. In streams with high densities of salmon, invertebrate biomass tended to decrease dramatically during salmon spawning. For example, in Bear Creek 2004, mayfly biomass decreased from 59.3 to 1.86 mg m^{-3} , stonefly biomass decreased from 14.5 to 0.18 mg m^{-3} , and dipteran biomass decreased from 6.71 to 0.57 mg m^{-3} in the

initial 9 days of salmon spawning (Fig. 4). In streams with the highest densities of salmon such as Yako, Bear and Pick Creeks, benthic insects such as mayflies and stoneflies did not recover following the conclusion of salmon spawning and were rarely detected for the remainder of the sampling season. In some streams and years with abundant salmon, other invertebrates (predominately planaria) increased following the end of salmon spawning, but invertebrate biomass post-salmon never recovered to pre-salmon levels. In contrast, in streams with few or no salmon, invertebrate biomass stayed fairly constant throughout the summer, although there was expected variability (Fig. 4). For example, in all 4 years in Cottonwood Creek salmon densities never exceeded $0.01 \text{ salmon m}^{-2}$, and total invertebrate biomass, composed predominantly of mayflies, stayed relatively constant throughout the entire summer season. No stream with low densities of salmon exhibited the dramatic decreases in late July or early August that were observed in streams with high densities of salmon (Fig. 5). In other streams with intermediate or variable sized runs, such as Lynx and Elva, invertebrate densities did not consistently decrease when salmon entered stream or recovered following salmon spawning.

Across all stream-years, invertebrate biomass decreased more during late July or early August in stream-years with high densities of salmon ($> 0.1 \text{ salmon m}^{-2}$) than stream-years with low densities of salmon (ANOVA, salmon effect; $F_1 = 33.05$, $P < 0.001$) (Fig. 6). However, individual taxa exhibited different seasonal patterns (ANOVA, taxa effect, $F_3 = 2.64$, $P = 0.05$). In stream-years with $> 0.1 \text{ salmon m}^{-2}$, caddis, mayfly, stonefly and dipteran biomass decreased between 75 and 86% during salmon spawning, on average, while biomass of other invertebrates, dominated by planaria, decreased 56% during salmon spawning, which was significantly less than the four previously mentioned taxa ($P < 0.001$ for all post-hoc paired t -tests).

Discussion

Salmon nest-digging intensely disturbs stream benthic communities (Figs 2, 4 and 5). This biotic disturbance often reduced algal and benthic invertebrate biomass by 75–85% (Figs 3 and 6). Salmon nest-digging, and the periodic post-spawn digging that maintains nests free of sediments, buries or dislodges algae and invertebrates for the duration of spawning. This bioturbation lasted over a month in some streams. Thus, salmon dramatically reduce algal and invertebrate biomass, confirming previous experimental (Moore *et al.* 2004) and observational studies (Hildebrand 1971; Field-Dodgson 1987; Minakawa & Gara 1999, 2003; Peterson & Foote 2000). Our study also identifies, for the first time, spawner densities necessary for salmon nest-digging to be a substantial source of disturbance. Above $0.1 \text{ salmon m}^{-2}$, salmon consistently decreased biomass of benthic communities, but below this threshold, had little noticeable impacts on benthic dynamics (Figs 3 and 6). These thresholds are of special concern in conservation biology (Huggett 2005) – human impacts that push the system or population over a threshold can lead to rapid ecosystem shifts.

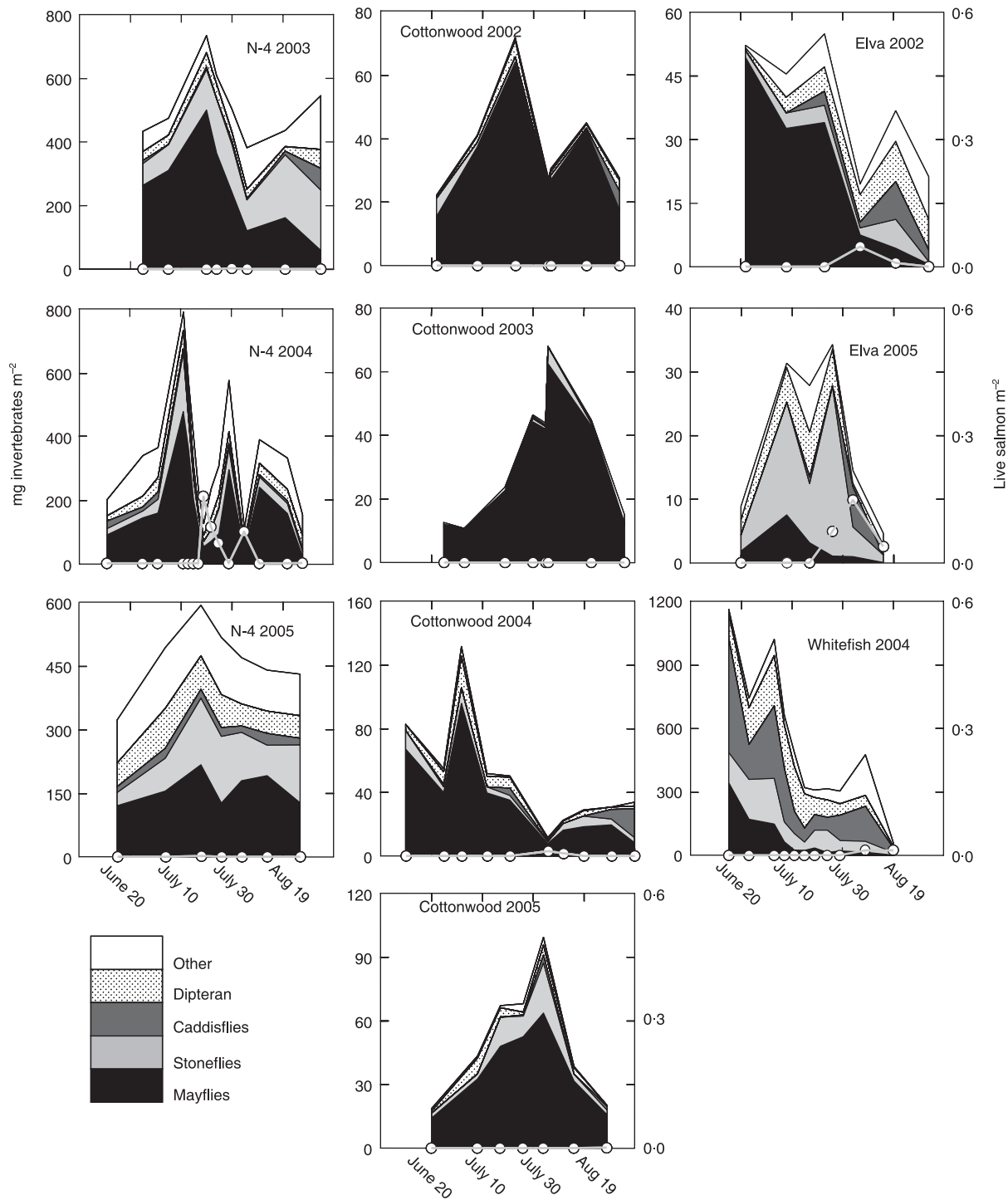


Fig. 4. Seasonal dynamics of invertebrate biomass in streams with no salmon or low salmon densities. Stacked areas correspond to biomass of different invertebrate taxa. Live salmon densities are portrayed by open circles and thick grey lines that correspond to the right y-axis. Note the different scales on the left y-axis.

Following conclusion of salmon spawning, algal biomass increased, sometimes approaching pre-spawning biomass by the end of the sampling season (Fig. 2). This recovery might simply be natural succession, as algal recovery is often rapid in streams following floods (e.g. Fisher *et al.* 1982). However, it is possible that salmon indirectly facilitate algal succession

via two mechanisms. First, nutrients from salmon carcasses may speed the recovery of algal communities. Previous studies have noted that nutrients from salmon carcasses increase algal accrual rates (e.g. Johnston *et al.* 2004). Indeed, a concurrent study found that spawning salmon were strongly associated with elevated levels of bioavailable nutrients in these streams

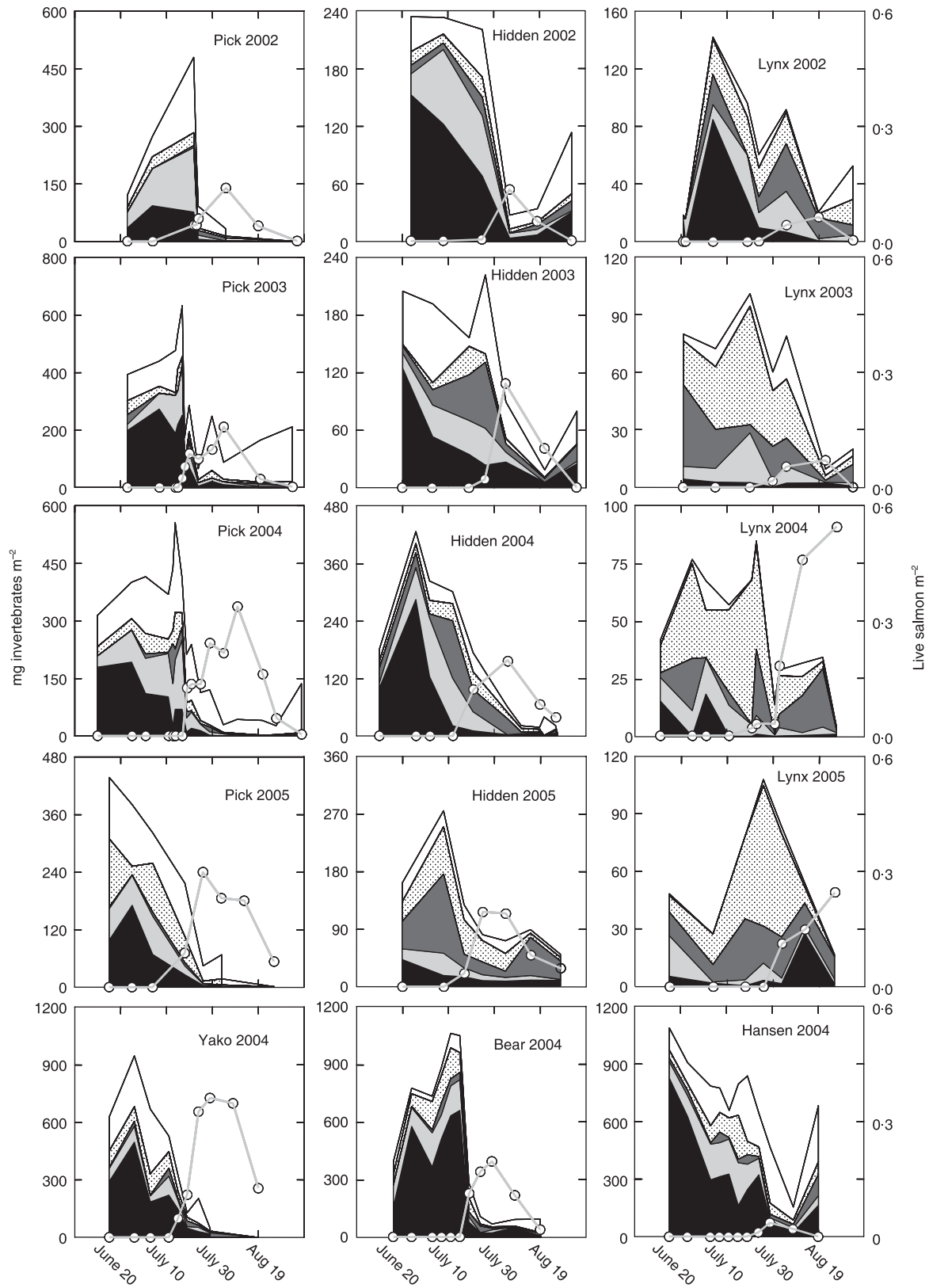


Fig. 5. Seasonal dynamics of invertebrate biomass in streams with high densities of salmon. Stacked areas correspond to biomass of different invertebrate groups. Live salmon densities are portrayed by open circles and thick grey lines that correspond to the right y-axis. Note the different scales on the left y-axis. See Fig. 4 for description of the shading patterns.

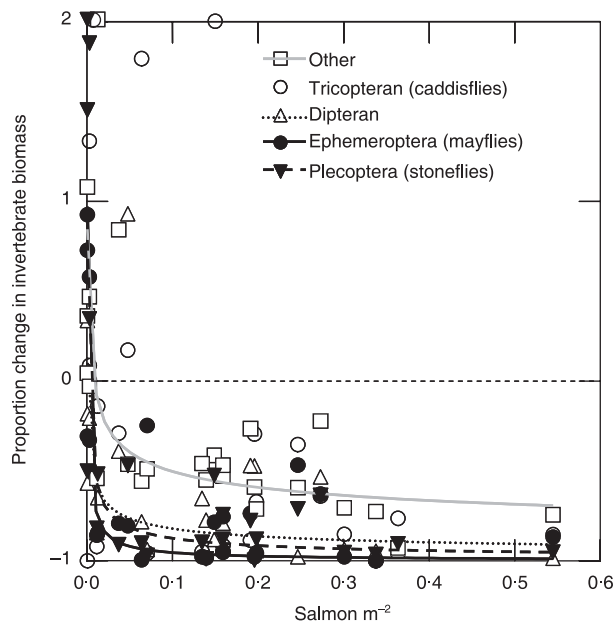


Fig. 6. Summary of the seasonal changes in invertebrate biomass as a function of salmon density, for the five invertebrate groups. Each point represents the proportional change in invertebrate biomass of a given stream-year, as a function of the maximum live salmon density of that stream-year. Proportional change was calculated as the proportion difference between average spring invertebrate biomass and invertebrate biomass during maximum salmon density. The dotted line through 0 represents stream-years with no change, below this line indicates a decrease, and above this line represents a stream-year with increased invertebrate biomass. The lines shown represent the best fit of a power functions. For streams without salmon, the period corresponding to maximum salmon densities was designated as occurring at the beginning of August. Note that the y -axis cut-off several data points that were subsequently located at $y > 2.0$.

(Moore *et al.* 2007). Second, salmon spawning might facilitate algal recovery by decimating populations of benthic invertebrate herbivores. Benthic invertebrate biomass failed to fully recover following disturbance from spawning salmon (Fig. 5), and benthic invertebrate herbivores can exert strong top-down control of periphyton in streams (e.g. Power 1990). Despite these possibilities, we did not observe any evidence that salmon positively impact algal biomass on long or short time frames. Algal biomass was not positively impacted by the spawning density the previous year. At a finer temporal resolution, increased salmon density only decreased algal biomass.

Salmon nest-digging also decreased biomass of benthic invertebrates, controlling their seasonal dynamics. In contrast with algal communities, invertebrate populations consistently failed to recover from this biotic disturbance during the same growing season. Indeed, invertebrate biomass in stream-years with high salmon densities never recovered to pre-salmon biomass the same year (Fig. 5). Salmon nest-digging likely directly reduces benthic invertebrate biomass by crushing or dislodging them (Peterson & Foote 2000). Decreases in aquatic insect densities during salmon spawning have been observed in both south-western (e.g. Peterson & Foote 2000) and south-eastern Alaskan streams (e.g. Lessard & Merritt

2006). Temporary decreases in caddisfly larval densities were associated with salmon spawning in Washington streams (Walter, Bilby & Fransen 2006). Thus, salmon nest-digging will modify the seasonal dynamics of benthic communities, with potential indirect impacts on predators of aquatic invertebrates such as stream-dwelling fishes.

Our study adds to the growing perception that salmon nest-digging is an important source of disturbance for benthic invertebrates, but that aquatic invertebrate life history mediates the impact of the disturbance. For example, it is possible that consistent and predictable salmon nest-digging has driven the evolution of benthic insect life-history phenologies. Predictable and severe floods can drive evolution of stream insect phenologies (Lytle 2002). A previous small-scale experimental exclusion of spawning salmon in two of the creeks in this study (Hidden Creek and Pick Creek) found that mayflies and stoneflies decreased during salmon spawning, even in plots where salmon were excluded from spawning (Moore *et al.* 2004). In contrast, planarians decreased in areas with spawning salmon but did not decrease in salmon exclusions plots, likely the result of direct disturbance. These data suggested that salmon nest-digging has direct negative local impacts on some taxa, namely planarians, but that mayfly and stonefly taxa disappear from streams, perhaps due to emergence into terrestrial adults, during or before salmon spawning. These results, coupled with the current studies' findings that aquatic insects only decrease in streams with many salmon, and that only planaria recover follow salmon spawning, suggests that some stream invertebrates may have life histories that are locally adapted to the predictable disturbance of salmon spawning. Previous studies have suggested this possibility that life history may mediate susceptibility to salmon disturbance. Minakawa & Gara (2003) observed that benthic invertebrate densities decreased by about 85% during chum salmon spawning in streams in Washington, but that populations of short-lived taxa quickly recovered following this disturbance. Similarly, Chaloner *et al.* (2004) and Lessard & Merritt (2006) observed that rapidly developing benthic invertebrates, namely chironomids, tended to be more dominant in stream reaches with high densities of salmon, as they recovered rapidly from the disturbance of their nest-digging, while longer-lived species, namely mayflies, were only negatively impacted by salmon. Concurrent analyses are explicitly investigating the impacts of salmon nest-digging on stream insect life-history characteristics.

This study suggests that the impacts of salmon on streams are likely context-dependent. In our location, we identified that beyond threshold densities, salmon primary impact stream benthic communities by acting as agents of disturbance. Indeed, disturbance from salmon nest-digging reduces the biomass of algae and invertebrates for much of the open water season to such an extent that there is little algae and insects remaining to capitalize on increased nutrients or carcass resources. These results contrast with the findings of previous studies that have primarily focused on how salmon may fertilize stream food webs from the bottom up (reviewed by Gende *et al.* 2002; Naiman *et al.* 2002). For example, Johnston *et al.* (2004) observed increases in periphyton biomass on cobble in

response to spawning salmon in natural streams in south-eastern Alaska. These contrasting findings highlight that these dominant species can have multiple impacts on coastal ecosystem that are likely context-dependent, simultaneously fertilizing and disturbing stream habitats. In addition to salmon density, factors that may influence the context dependency include stream characteristics such as light availability, flow regime, substrate size, background nutrient levels, as well as the timing and species identity of the salmon run (Tiegs *et al.* in press). Indeed, it has proved challenging to understand the context dependency of the impacts of these dominant species (e.g. Ambrose, Wilzbach & Cummins 2004).

There have been suggestions that salmon-derived nutrients may increase productivity of juvenile salmon by fertilizing stream food webs, leading to a positive feedback mechanism between adult returns and juvenile production (Stockner, Rydin & Hyenstrand 2000; Bilby *et al.* 2001). This perception that salmon populations increase biomass of stream benthic food webs is often based on small-scale carcass addition experiments (e.g. Chaloner & Wipfli 2002), which do not incorporate disturbance from nest-digging salmon. Salmon carcass addition and fertilization programmes, used as a restoration tool for streams with impoverished salmon populations (Compton *et al.* 2006), fail to account for biogenic disturbance from spawning salmon, and capture little reality of how salmon impact streams via manifold pathways.

Human activities are altering disturbance regimes via multiple factors. Most of the large river systems in the world are now dammed (Nilsson *et al.* 2005), altering flood regimes (Poff *et al.* 1997). Floods can increase fish production, move sediments and nutrients, and control seasonal dynamics (Bayley 1995; Poff *et al.* 1997). Thus, alteration of disturbance regimes can have wide-reaching consequences to stream ecosystems and the services they provide. Here we show that nest-digging salmon are also an important component of coastal stream disturbance regimes. Human activities that drive salmon populations below threshold densities, as has likely happened in many coastal streams (NRC 1996), will lead to fundamental changes in the disturbance regimes and the rearrangement of seasonal dynamics of benthic stream communities.

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References

Adams, J. (2004) *Guide to Pacific Northwest Macroinvertebrate Monitoring*. The Xerces Society, Portland, OR. Available online or on CD at <http://www.xerces.org/>

Ambrose, H.E., Wilzbach, M.A. & Cummins, K.W. (2004) Periphyton response to increased light and salmon carcass introduction in northern

California streams. *Journal of the North American Benthological Society*, **23**, 701–712.

Baker, T.T., Fair, L.F., Clark, R.A. & Hasbrouck, J.J. (2006) *Review of Salmon Escapement Goals in Bristol Bay, 2006*. Fisheries Manuscript no. 06–05, Anchorage. Alaska Department of Fish and Game, Alaska.

Bayley, P.B. (1995) Understanding large river floodplain ecosystems. *BioScience*, **45**, 153–158.

Bilby, R.E., Fransen, B.R., Walter, J.K., Cederholm, C.J. & Scarlett, W.J. (2001) Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific Salmon. *Fisheries (Bethesda)*, **26**, 6–14.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Chaloner, D.T. & Wipfli, M.S. (2002) Influence of decomposing Pacific salmon carcasses on macroinvertebrate growth and standing stock in southeastern Alaska streams. *Journal of the North American Benthological Society*, **21**, 430–442.

Chaloner, D.T., Lamberti, G.A., Merritt, R.W., Mitchell, N.L., Ostrom, P.H. & Wipfli, M.S. (2004) Variation in responses to spawning Pacific salmon among three south-eastern Alaska streams. *Freshwater Biology*, **49**, 587–599.

Coleman, F.C. & Williams, S.L. (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution*, **17**, 40–44.

Compton, J.E., Andersen, C.P., Phillips, D.L., Brooks, J.R., Johnson, M.G., Church, M.R., Hogsett, W.E., Cairns, M.A., Rygielwicz, P.T., McComb, B.C. & Shaff, C.D. (2006) Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. *Frontiers in Ecology and the Environment*, **4**, 18–26.

Field-Dodgson, M.S. (1987) The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. *Hydrobiologia*, **154**, 3–11.

Fisher, S.G., Gray, L.J., Grimm, N.B. & Busch, D.E. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*, **52**, 93–110.

Flecker, A.S. (1997) Habitat modification by tropical fishes: Environmental heterogeneity and the variability of interaction strength. *Journal of the North American Benthological Society*, **16**, 286–295.

Flecker, A.S., Feifarek, B.P. & Taylor, B.W. (1999) Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. *Copeia*, **1999**, 495–500.

Gende, S.M., Edwards, R.T., Willson, M.F. & Wipfli, M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, **52**, 917–928.

Gottesfeld, A.S., Hassan, M.A., Tunniffcliff, J.F. & Poirier, R.W. (2004) Sediment dispersion in salmon spawning streams: the influence of floods and salmon redd construction. *Journal of the American Water Resources Association*, **40**, 1071–1086.

Hildebrand, S.G. (1971) The effect of coho spawning on the benthic community of the Platte River, Benzie County, Michigan. *Transactions of the American Fisheries Society*, **100**, 61–68.

Huggert, A.J. (2005) The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation*, **124**, 301–310.

Johnston, N.T., MacIsaac, E.A., Tschaplinski, P.J. & Hall, K.J. (2004) Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 383–403.

Lessard, J.L. & Merritt, R.W. (2006) Influence of marine-derived nutrients from spawning salmon on aquatic insect communities in southeast Alaskan streams. *Oikos*, **113**, 334–343.

Lytle, D.A. (2002) Flash floods and aquatic insect life-history evolution: evolution of multiple models. *Ecology*, **83**, 370–385.

Marriott, R.A. (1964) *Stream Catalog of the Wood River Lake System, Bristol Bay, Alaska*. United States Fish and Wildlife Service, Washington, DC.

McIntyre, P.B., Jones, L.E., Flecker, A.S. & Vanni, M.J. (2007) Fish extinctions alter nutrient recycling in tropical freshwaters. *Proceedings of the National Academy of Sciences*, **104**, 4461–4466.

Merritt, R.W. & Cummins, K.W. (eds) (1996) *An Introduction to the Aquatic Insects of North America*, 3rd edn. Kendall. Hall Publishing Co., Dubuque, IA.

Minakawa, N. & Gara, R.I. (1999) Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. *Journal of Freshwater Ecology*, **4**, 327–335.

Minakawa, N. & Gara, R.I. (2003) Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific Northwest. *Transactions of the American Fisheries Society*, **132**, 598–604.

- Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Hames, D. & Quinn, T.P. (1996) Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1061–1070.
- Moore, J.W. (2006) Animal ecosystem engineers in streams. *Bioscience*, **56**, 237–246.
- Moore, J.W., Schindler, D.E. & Scheuerell, M.D. (2004) Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia*, **139**, 298–308.
- Moore, J.W., Schindler, D.E., Carter, J.L., Fox, J., Griffiths, J. & Holtgrieve, G.W. (2007) Biotic control of stream ecosystem fluxes: spawning salmon control export of nutrients and matter in Alaskan streams. *Ecology*, **88**, 1278–1291.
- Naiman, R.J., Bilby, R.E., Schindler, D.E. & Helfield, J.M. (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**, 399–417.
- Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science*, **308**, 405–408.
- NRC (National Resource Council). (1996) *Upstream: Salmon Society in the Pacific Northwest*. National Academy Press, Washington, DC.
- Peterson, D.P. & Foote, C.J. (2000) Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. *Transactions of the American Fisheries Society*, **129**, 924–934.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E. & Stromberg, J.C. (1997) The natural flow regime: a paradigm for river conservation and restoration. *Bioscience*, **47**, 769–784.
- Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Reviews of Ecology and Systematics*, **28**, 289–316.
- Power, M.E. (1990) Effects of fish in river food webs. *Science*, **250**, 811–814.
- Quinn, T.P. (2005) *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press, Seattle, WA.
- Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. & Srivastava, D.R. (2004) Extinction and ecosystem function in the marine benthos. *Science*, **306**, 1177–1180.
- Steinman, A.D., Lamberti, G.A. & Leavitt, P.R. (2006) Biomass and pigments of benthic algae. *Methods in Stream Ecology* (eds R. Hauer & G.A. Lamberti), pp. 357–380. Elsevier Inc., Burlington, MA.
- Stockner, J.G., Rydin, E. & Hyenstrand, P. (2000) Cultural oligotrophication: causes and consequences for fisheries resources. *Fisheries (Bethesda)*, **25**, 7–14.
- Taylor, B.W., Flecker, A.S. & Hall, R.O. Jr (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science*, **313**, 834–836.
- Tiegs, S.D., Chaloner, D.T., Levi, P., Rüegg, J., Tank, J.L. & Lamberti, G.A. (in press) Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecological Applications*.
- Walter, J.K., Bilby, R.E. & Fransen, B.R. (2006) Effects of Pacific salmon spawning and carcass availability on the caddisfly *Ecclisomyia conspersa* (Trichoptera: Limnephilidae). *Freshwater Biology*, **51**, 1211–1218.
- Wipfli, M.S., Hudson, J. & Caouette, J. (1998) Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1503–1511.
- Wright, J.P. & Jones, C.G. (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *Bioscience*, **56**, 203–209.

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