Oecologia (2004) 139: 298–308
DOI 10.1007/s00442-004-1509-3

ECOSYSTEM ECOLOGY

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Disturbance of freshwater habitats by anadromous salmon in Alaska

Received: 2 June 2003 / Accepted: 16 January 2004 / Published online: 3 March 2004

Abstract High densities of habitat modifiers can dramatically alter the structure of ecosystems. Whereas spawning sockeye salmon (*Oncorhynchus nerka*) dig nests that cover over 2 m^2 and are at least 20 cm deep, and can spawn at high densities, relatively little attention has been devoted to investigating the impacts of this disturbance. We hypothesized that this temporally and spatially predictable bioturbation has large impacts on the coastal aquatic habitats used by sockeye. We experimentally investigated the impacts of disturbance caused by spawning sockeye in two streams and two lakes in Alaska by excluding salmon from 2.25 m^2 plots where they traditionally spawn. We sampled exclusions and control plots before, during, and after spawning. During sockeye spawning, fine sediment accumulated in areas where sockeye were excluded from spawning. In addition, sockeye spawning significantly decreased algal biomass by 80% compared to exclusion plots. We found mixed effects of spawning on the invertebrate assemblage. Tricladida and Chironomidae densities increased by 3x in exclusion plots relative to control plots in one creek site. However, for most taxa and sites, invertebrate densities declined substantially as spawning progressed, regardless of experimental treatment. Habitat modification by spawning salmon alters both community organization and ecosystem processes.

Keywords Benthic invertebrates · Bioturbation · Ecosystem engineer · Habitat modification · *Oncorhynchus*

Introduction

Disturbances shape the community structure and ecosystem processes of aquatic habitats (Resh et al. 1988; Bayley 1995; Wootton et al. 1996). For example, floods can constrain the life-history strategies of aquatic invertebrates (Gray and Fisher 1981; Lytle 2000, 2001), alter food web dynamics (Wootton et al. 1996), increase riverine productivity and riparian connectivity (Bayley 1995), and possibly drive shifts between alternate ecosystem states (Scheffer et al. 2001). Although disturbances are usually considered abiotic perturbations, the activities of organisms that physically modify habitats can also be important disturbances (Myers 1977; Lawton and Jones 1995).

Organisms that physically change the habitat and physical structure of ecosystems and indirectly or directly alter the availability of resources for other organisms are termed habitat modifiers (Power 1997) or ecosystem engineers (Jones et al. 1994, 1997; Lawton and Jones 1995). For example, beavers (*Castor canadensis*) build dams that flood upstream areas, increasing carbon storage (Naiman et al. 1986), habitat complexity, and fish diversity (Snodgrass and Meffe 1998). Some species of benthic aquatic insects, such as hydropsychid caddis flies, produce silk that anchors and stabilizes substrates (Statzner et al. 1999).

Bioturbation by habitat modifiers can be a substantial disturbance. For example, alligators (*Alligator mississippiensis*) dig wallows that provide critical refuge for aquatic organisms during periods of low water (Loveless 1959). The activities of other aquatic invertebrates, such as stoneflies (Statzner et al. 1996) and crayfish (Statzner et al.

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2000), increase rates of fine sediment erosion. Detritivores such as fish (Flecker 1996; Power 1990) and shrimp (Pringle and Blake 1994; Crowl 2001; March et al. 2002) reduce accumulation of fine sediments in streams. Numerous species of freshwater fishes dig nests in which they lay their eggs, producing isolated patches of disturbed substrate (Carpenter and McCreary 1985; Thorp 1988; Thorp et al. 1989; Kupriyanova and Bailey 1998; Peterson and Foote 2000). However, the impacts of bioturbation by habitat modifiers have infrequently been investigated through experimental manipulations (Jones et al. 1997), although there are notable exceptions (e.g., Myers 1977; Brenchley 1981; Power 1990; Pringle and Blake 1994; Flecker 1996; Statzner et al. 1996; Crowl 2001; March et al. 2002). Here, we present results of an experiment that examined the role of bioturbation by nest-digging sockeye salmon as a source of disturbance to freshwaters.

Due to their anadromous and semelparous life-history, Pacific salmon act as vectors of marine-derived nutrients and energy to coastal ecosystems. These salmon nutrients may be critical in maintaining coastal productivity and biodiversity (reviewed by Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). In addition, nest-digging by anadromous salmon may also have large impacts on community structure in freshwater habitats used for spawning. Pacific salmon (*Oncorhynchus* spp) accumulate over 95% of their mass in the ocean before they return to freshwaters, where they cease feeding, spawn, and eventually die (Groot and Margolis 1991). This migration can allow salmon to be disproportionately large-bodied and abundant compared to resident fishes in the freshwaters where they spawn (Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). A female Pacific salmon digs at least one large nest (redd) in which she lays and buries her eggs. Depending on the size, species, and location of spawning salmon, a single salmon redd can cover between 1 m^2 and 17 m^2 (Groot and Margolis 1991), and be up to 35 cm deep (Steen and Quinn 1999). In three creeks in the Wood River system, Alaska, female sockeye salmon (*Oncorhynchus nerka*) dig nests in the gravel substrate that cover around 2.1 to 4.1 m^2 and are on average 20 cm deep (Steen and Quinn 1999; Peterson and Foote 2000). Sockeye attain densities in these creeks of at least 1,500 fish per km of the entire stream length (Peterson and Foote 2000).

Even though healthy populations of anadromous salmon often spawn at high densities and dig large nests, the impacts of this disturbance are relatively unknown. Although lacking rigorous controls, previous observational studies have suggested that these recently disturbed patches may be characterized by lower levels of fine sediment (Kondolf et al. 1993; Montgomery et al. 1996) and reduced abundances of benthic flora and fauna (Hildebrand 1971; Field-Dodgson 1987; Minakawa and Gara 1999, 2003; Peterson and Foote 2000).

To investigate the impacts of salmon spawning on benthic habitats, we experimentally excluded sockeye salmon (*O. nerka*) from plots and compared the physical substrate and benthic communities in exclusions to control areas where salmon were allowed to spawn during the summer of 2001. We asked the following questions: How does salmon nest-digging impact the physical characteristics and community assemblage of benthic habitats? How do these impacts differ among spawning sites with different salmon densities? How do these impacts differ between lake and stream spawning sites? By experimentally isolating the dramatic impacts of salmon nest-digging on spawning habitats in a healthy population, we can add to our understanding of the consequences of the salmon population declines that characterize the Pacific coastal ecosystems of the lower 48 states of the USA.

Materials and methods

Study sites

We investigated the impacts of sockeye salmon spawning in two streams and two lakes located within the Wood River drainage in southwestern Alaska. This 300,000 ha river system is an important spawning and nursery system for anadromous sockeye salmon (*O. nerka*) in the Bristol Bay region. An average of around 2.5 million adult sockeye return to spawn in the Wood River system every year, of which an average of 1.5 million sockeye are harvested by the Bristol Bay salmon fishery (University of Washington Alaska Salmon Program, unpublished data). Although timing varies among sites, sockeye spawning in the Wood River system starts in mid-July, peaks in August, and ends in September (Marriott 1964). Although there are occasional pink (*O. gorbuscha*), king (*O. tshawytscha*), coho (*O. kisutch*), and chum salmon (*O. keta*) in this system, none were observed in the experimental reaches during the duration of the experiment. The Wood River system is the study location of the Alaska Salmon Program of the University of Washington, which started monitoring Bristol Bay sockeye populations in 1947 and has since maintained a series of long-term studies of sockeye salmon in this ecosystem.

Our four study sites are typical examples of the dozens of streams and beach sites in the Wood River system used by spawning sockeye. Lynx Lake (59°29′42″N, 158°55′12″W) is 176 ha, while Hidden Lake (59°32′54″N, 158°45′42″W) is 20.2 ha. In both lakes, the majority of spawning occurs along several beaches in water less than 1.5 m deep. Hidden Lake Creek (59°32′54″N, 158°45′42″W), which drains Hidden Lake, is 1.4 km long, averages 4.8 m wide and 27 cm deep (Marriott 1964). An average of 1,800 sockeye spawn in Hidden Lake Creek every year (University of Washington Alaska Salmon Program, unpublished data). Pick Creek (59°33′00″N, 159°04′18″W) averages around 6,000 spawning sockeye along its 4.1 km length. Pick Creek averages 5.1 m wide and 46 cm deep (Marriott 1964). Although sockeye dominate the fish assemblage, both streams and lakes sustain populations of native resident fishes, including rainbow trout (*O. mykiss*), Arctic grayling (*Thymallus arctus*), Arctic char (*Salvelinus alpinus*), Dolly Varden (*S. malma*), sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), and sculpins (*Cottus*spp). These fish are all predators and have not been observed to disturb substrates during feeding. None of these fish spawn during the 2 months of the experiment.

Experimental design

The objective of this study was to experimentally isolate the local impacts of salmon nest-digging on streams and lakes. At each of the two streams and two lakes, we selected one stream reach or one lake beach that was roughly 100 m long where sockeye traditionally spawn every summer. Within each of these spawning sites, we assessed the impacts of salmon spawning by comparing plots of unmanipulated densities of spawning sockeye to plots where salmon were excluded from spawning. Within each of the four experimental areas, we selected 12, 2.25 m^2 plots (1.5×1.5 m), which approximated the areal size of an average sockeye salmon redd (Steen and Quinn 1999). Each plot was randomly assigned to one of three treatments: salmon exclusion (no spawning sockeye), exclusion control (unmanipulated densities of sockeye with a partial cage to control for possible exclusion effects), and reference plots (unmanipulated densities of sockeye with no cage structure). Thus, at each experimental site, there were four exclusion, four controls, and four reference sites. Although it would have been preferable to manipulate entire reaches of the streams and beaches, we wanted to minimize any adverse effects on the entire sockeye spawning populations.

Exclusions and exclusion controls were constructed with steel fencing (mesh size 4×8 cm), anchored by at least eight rebar stakes driven 0.5 m deep into the sediment. Plots were constructed 18–22 June 2001, around 6–8 weeks prior to the arrival of adult salmon at the spawning sites. The mesh allowed small fish and invertebrates to move through exclusions, but excluded adult sockeye salmon. Exclusions had four continuous sides, and were uncovered on the top and entrenched at the bottom. The top of the fencing extended out of the water to prevent salmon from entering over the top. Controls were similar to exclusions except that they were open on two adjacent sides. Controls allowed salmon access to the plot areas, but controlled for possible effects of the structure and construction on water flow. The controls were open on the downstream side in stream sites, and the direction of the opening was determined randomly in lake sites. Reference plots were marked by rebar posts, and did not have any mesh. We experimentally isolated effects of salmon spawning by comparing salmon exclusions to areas where sockeye were allowed to spawn (controls and reference plots) before, during, and after salmon spawning. Because mesh on exclosures and controls in stream sites accumulated debris, we cleaned the mesh every 3–10 days.

As with any exclusion experiment, cage effects may confound the experimental results (Peterson 1979; Peckarsky and Penton 1990). Many cage studies exclude a suite of mobile organisms, making it difficult to isolate causation. However, because of the large mesh size (4×8 cm), virtually all of the resident fishes were small enough to move in and out of the exclusions. We frequently observed small resident fishes freely entering and exiting exclusions. In addition, all other fishes are not detritivores and do not spawn during July and August. Therefore, we believe that our exclusions did not alter benthic assemblages by excluding organisms other than adult spawning salmon. In addition, it is unlikely that the observed differences between exclusions and controls and references are driven by altered water dynamics. Using a flow meter (Swoffer brand, horizontal propeller) at a depth that was 50% of the depth at that location, we compared flows in front of plots to flows inside plots and calculated the change in water velocity. We compared flows during two sampling periods for each of four replicates for each treatment; therefore we have 6–8 estimates of how flow changed for each treatment/creek combination. In Pick Creek, exclusions tended to decrease mean water velocity by an average of 16.6% such that water velocity inside exclusions averaged 0.46 ±0.107 m s^{-1} (this and the following are ±1 SD). Controls tended to decrease mean water velocity 19.6% to 0.49±0.168 m s^{-1}, while references also tended to decrease water velocity 9.0% to 0.58 ±0.07 m s^{-1}, but differences between treatments were not significant (ANOVA, $F_{2,17}$=0.342, P=0.715). Similarly, in Hidden Lake Creek, exclusions tended to decrease mean water velocity 5.0% such that water velocity inside exclusions averaged 0.32±0.075 m s^{-1}, controls tended to increase mean water velocity 3.2% to 0.51 ±0.046 m s^{-1}, while references tended to slightly decrease mean water velocities 0.4% to 0.52±0.131 m s^{-1}, but again none of these differences were significant (ANOVA, $F_{2,21}$=0.307, P=0.739).

Data collection

We sampled each site every 3 to 4 weeks from 27 June to 29 August 2001, for a total of three dates corresponding to before, during, and after salmon spawning. The first date was 6–14 days after the plots were constructed. We minimized the cumulative disturbance of our sampling efforts by avoiding walking in the plots, as well as by sampling a different location within the plot on each date. During sampling, we assessed local salmon densities, benthic substrate composition, benthic invertebrate community, and algal abundance.

Every 3–10 days (including at each sampling occasion) we counted the number of live sockeye salmon in each experimental site. The experimental sites were defined as the area of stream or lake that encompassed all of the plots. Salmon were not easily spooked by observer presence and were easily observed because of their large body size and bright coloration, and the shallow depth of the water. Salmon numbers were converted to densities by dividing the number of observed salmon by the area of the experimental site.

We characterized the size composition of substrates by taking a 15 cm deep grab sample (hemispherical, radius of 15 cm). The substrate was subsequently passed through a set of sieves, partitioning the substrate into the following size classes: <0.6 mm, 0.6–1.98 mm, 1.98–5.6 mm, 5.6–9.52 mm, 9.52–22.5 mm, and >22.5 mm. After draining the water, we recorded the total wet mass of each size class of substrate. These raw masses were converted to the proportion of the total mass. We focused our analyses on the proportion of sediments that were <0.6 mm in diameter, which we refer to as fine sediment.

We estimated periphyton biomass (chlorophyll-*a*cm^{-2}) on substrates at each site. For Hidden Lake Creek, Pick Creek, and Lynx Lake, periphyton on rocks could be measured directly, but for Hidden Lake, rocks were rare so we used 121 cm^2 ceramic tiles as a colonization substrate for algae (e.g., Flecker et al. 2002). Where rocks were available, at each sampling period we haphazardly selected three rocks larger than 30 mm in diameter from the plot. We placed tiles in early July and harvested them on the last sampling date. Rocks and tiles were brought back to the field station lab, scrubbed with a small brush, and vigorously rinsed. We combined the rinsed portion of the three rocks from each plot and filtered this 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* using fluorometry (Marker et al. 1980). 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. We assumed that periphyton only colonized the top half of each rock.

On each sampling occasion, we also characterized the composition and density of the benthic invertebrate community using a Surber sampler (0.09 m^2 quadrat, mesh size 250 μm) by agitating the benthos to a depth of 10 cm. In lakes, we manually generated flow to push the resuspended benthos through the Surber sampler. We took one Surber sample per plot per time point. Samples were preserved in 70% ethanol, stained with Eosin Y, and identified at a later date. Invertebrates were identified to the lowest feasible classification at 10× under a dissecting microscope according to the following references (Edmunds et al. 1976; Wiggins 1977; Merritt and Cummins 1978; Thorp and Covich 1991; Stewart and Stark 1993). For the following analyses, the highest taxonomic resolution was genus, but most invertebrates were identified to family. We did not include incidental terrestrial invertebrates or empty insect cases in our analyses.

Data analysis

We used both univariate and multivariate statistics to quantify the impacts of salmon spawning on stream and lake benthos. We used two-way repeated-measures ANOVA (rmANOVA) with treatment and site as factors to analyze the change in treatments through time. Our three sampling dates were approximately equally spaced through time, and functionally represent three periods of interest: before, during, and after salmon spawning. We used separate rmANOVAs to detect changes in three response variables: proportion of fine sediment, algal biomass, and densities of invertebrate taxa.

To normalize the data prior to analyses, fine sediment data were $\sqrt{\sqrt{x}}$ transformed, while algal and invertebrate data were $\ln(x+1)$ transformed. These transformations led to statistically equal variances for all time periods of the silt data (O'Brien's test, $P>0.05$), whereas prior to transformation the silt data had unequal variances ($P<0.05$). Similarly, although algal data already had statistically equal variances prior to transformation, transformation improved homogeneity (e.g., for before time period: prior to transformation, $F_{2,45}=0.78$, $P=0.48$; post-transformation $F_{2,45}=0.52$, $P=0.60$). In general, transformation improved homogeneity of variances of the invertebrate data (improved F statistic 75% of different time/site combinations); as a result all but one of the 12 different time/site combinations had equal variances after transformation ($P>0.05$). In addition, one-sample Kolmogorov-Smirnov tests revealed that transformations always improved normality. Even so, some of the invertebrate and algal data were significantly different from normal ($P<0.05$), although transformed silt data were normal ($P>0.05$). However, ANOVA is relatively robust to such minor departures in normality (Zar 1999).

We did not include Hidden Lake in the algal rmANOVA because there was only one time point from this site. Because invertebrate assemblages differed drastically between sites, we performed repeated-measures analysis separately for each site on the densities of the four most abundant taxa of each site. All data used for repeated-measures tests conformed to the sphericity, or circularity, assumption (Sphericity test, $P>0.05$) that is critical for repeated-measures ANOVAs (von Ende 1993). For repeated-measures ANOVAs that had significant results, we ran post-hoc ANOVAs and compared pairs using Tukey HSD tests. We used JMP and SYSTAT programs to perform these analyses.

In addition, because the prior analyses of invertebrate densities did not include all details of the invertebrate assemblages and considered each taxon separately, we used multivariate statistics to depict changes in the entire invertebrate assemblage. Bray-Curtis coefficients were used to calculate a similarity matrix between samples based on counts of different species in the invertebrate assemblage (McCune and Grace 2002). In the rare case (four of 144 samples) that a sample did not contain any invertebrates, we excluded this sample from the similarity matrix. We used analysis of similarities (ANOSIM; Clarke and Warwick 1994) to test for differences between invertebrate assemblages based on the rank similarities from the Bray-Curtis similarity matrices, with 999 iterations. Because all sites were different and ANOSIM is constrained to analyze only one or two factors, we analyzed each site separately and considered time and treatment as factors. We ran ANOSIMs on all samples from all dates, using site as a factor. In addition, we ran a two-factor ANOSIM for each site considering date and treatment as factors. Subsequently, in cases where there were significant differences, we used ANOSIM post-hoc tests, with Bonferroni corrections to account for multiple comparisons, to evaluate differences between dates, sites, or treatments. We performed these multivariate analyses using PRIMER software (Clarke and Warwick 1994).

When ANOSIM revealed significant differences between factors, we used the Species Contributions to Similarity (SIMPER) function in PRIMER to identify which taxa were responsible for the observed differences in assemblages. SIMPER uses the Bray-Curtis similarity matrix to calculate how much each taxon contributes to the observed dissimilarities between groups.

We used nonmetric multidimensional scaling (nMDS) to visualize how invertebrate assemblages differed between times and treatments. This technique is the preferred method to portray community patterns graphically in two dimensions (Clarke 1993; McCune and Grace 2002) and has been used to illustrate differences between aquatic invertebrate assemblages (e.g., Thompson and Townsend 2003). nMDS uses an iterative process that searches for the ordination of samples that best represents the precalculated matrix of similarity between samples (Clarke 1993). nMDS seeks to minimize "stress", which is the departure of the distances between samples in the ordination from the distances calculated between samples in the original similarity matrix (Clarke 1993). In order to visualize how invertebrate communities changed across time and treatments, we ran nMDS for each site separately.

Results

Densities of salmon differed among study sites. Within the study sites, Pick Creek had the highest peak density of spawners, with 0.35 salmon m^{-2}. Hidden Lake Creek densities were second highest, with 0.23 salmon m^{-2}. Assuming a 50:50 sex ratio, non-overlapping redds, and that female salmon dig redds that average between 2.1 and 4 m^2 (Steen and Quinn 1999; Peterson and Foote 2000), between 37% and 72% of Pick Creek was covered by salmon redds at the peak of spawning in 2001. Given the same assumptions, between 22% and 43% of the area of the experimental site in Hidden Lake Creek was covered by salmon redds. In addition, just the swimming action of these large fish in the small creeks and shallow beaches appeared to result in a substantial disturbance of fine sediments and benthos.

Salmon did not avoid control or reference plots and were frequently observed actively digging, spawning, and swimming in these plots. Over the entire course of the experiment, we observed only a single salmon in an exclusion. This salmon had dug under the fencing and was promptly removed. Within the experimental sites, both lakes had lower densities of spawning salmon, with less than 0.05 salmon m^{-2}. In Lynx Lake, densities were especially low, and only a few salmon dug nests in the experimental reach. Spawner densities peaked in early August in all four sites.

Impacts of salmon spawning on local substrate

Before salmon spawned, there were no significant differences in the proportion fine sediment by weight between treatments (ANOVA, $P>0.30$; Fig. 1). However, salmon spawning reduced fine sediment accumulation, indicated by a significant treatment effect (Table 1; Fig. 1). Specifically, during or after salmon spawning, levels of fine sediment were higher in exclusions than in areas with spawning sockeye in Pick Creek, Hidden Lake Creek, and Hidden Lake (ANOVA, $P<0.05$; Fig. 1), indicated by a significant time×treatment interaction (Table 1) and Tukey post-hoc contrasts (Fig. 1). For example, in Pick Creek, levels of fine sediment were 5× higher in exclusions than controls and references after salmon had finished spawning (Fig. 1). Time itself was not a significant factor in influencing substrate composition (Table 1). Different sites had different levels of fine sediment (Table 1): on average, Hidden Lake had the most fine sediment, followed by Pick Creek, Hidden Lake Creek, and Lynx Lake (Fig. 1).

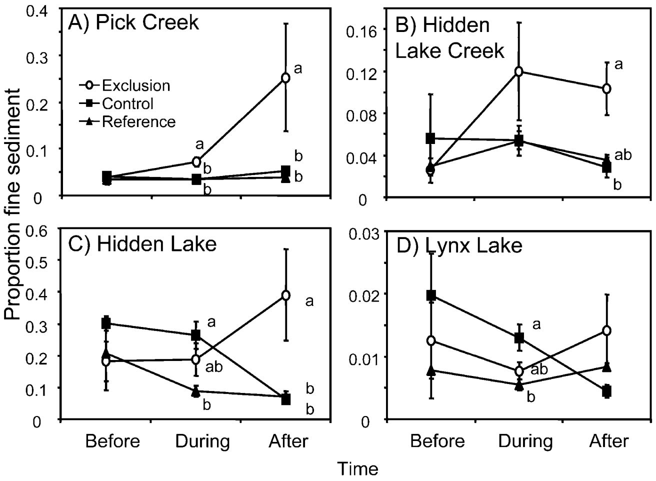

Fig. 1A–D The proportion of fine sediment <0.6 mm in the three treatments through time, at each of the four sites. Data presented are means±1 SE. Significant differences ($P<0.05$) between treatments at a given time and site were determined with post-hoc Tukey's multiple comparisons and are designated with a different *letter* above the point

Table 1 Results from the repeated-measures ANOVA (before, during, and after salmon spawning) on fine sediment (proportion <0.6 mm)

Source	*df*	*F*	*P*
Fine sediment			
Treatment	2	10.14	0.0003
Site	3	73.16	<0.0001
Site×treatment	6	1.31	0.28
Time	2	1.24	0.30
Time×treatment	4	8.63	<0.0001
Time×site	6	4.00	0.0017
Time×site×treatment	12	1.42	0.18

Impacts of salmon spawning on periphyton

Salmon spawning had a significant effect on changes in algal biomass in plots, but these effects were dependent upon site as indicated by a significant three-way interaction (time×site×treatment) (Table 2). Before salmon spawned, algal biomass, as indicated by chlorophyll-*a*cm^{-2}, was similar across treatments in all sites but Hidden Lake, where we did not obtain "before" data (ANOVA, $P>0.25$; Fig. 2). However, as salmon initiated spawning, periphyton biomass in different treatments diverged as indicated by a significant time×treatment interaction (Table 2; Fig. 2). For example, algal biomass was 5× higher in exclusion plots than both reference and control plots during salmon spawning in Pick Creek (ANOVA, $F_{2,9}=16.2$, $P=0.001$; Tukey's post-hoc tests, exclusions vs. references, $P=0.001$, exclusions vs. controls, $P=0.001$; Fig. 2). In comparison, algal biomass peaked after salmon spawning in Hidden Lake Creek: exclusions had twice as much algae as reference and control plots (ANOVA, $F_{2,9}=5.58$, $P=0.03$; Tukey's post-hoc tests, exclusions vs. references, $P=0.041$, exclusions vs. controls, $P=0.076$; Fig. 2). However, there were no significant differences among treatments within Hidden Lake and Lynx Lake (Fig. 2). Sockeye thus had negligible effects on periphyton in lakes sites, but substantial effects in stream sites.

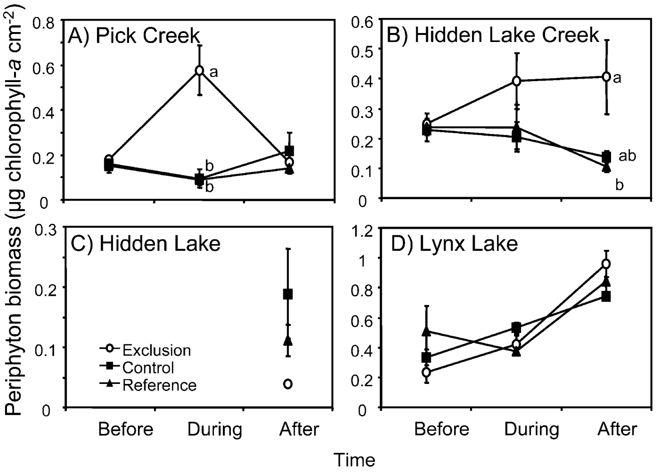

Fig. 2A–D Algal biomass in the three treatments before, during and after peak sockeye spawning, at the four study sites. Data presented are means±1 SE. Because Hidden Lake did not have suitable natural substrate for periphyton, Hidden Lake data is only available from algal biomass on tiles at the end of the experiment. Significant differences ($P<0.05$) between treatments at a given time and site were determined with post-hoc Tukey's multiple comparisons and are designated with a different *letter* above the point. The error bars for the Hidden Lake exclusion plots are so small as to be hidden from view

Impacts of salmon spawning on benthic invertebrate assemblages

The four most abundant taxa at each site numerically comprised between 82 and 97% of the total invertebrate assemblage, depending on the site. Because the four most abundant taxa differed across sites, we ran rmANOVAs with treatment as a factor for each of the top four taxa at each of the sites. In Pick Creek, there was a significant time×treatment interaction for Tricladida (Planaria) ($F_{4,16}=5.9$, $P<0.01$) and Chironomidae ($F_{4,16}=5.7$, $P<0.01$), indicating that treatments diverged over time

Table 2 Results from the repeated-measures ANOVA on algal biomass (µg chlorophyll-*a*cm^{-2})

Source	*df*	*F*	*P*
Algal biomass			
Treatment	2	9.48	0.0008
Site	2	93.65	<0.0001
Site×treatment	4	4.14	0.0096
Time	2	6.96	0.004
Time×treatment	4	3.52	0.013
Time×site	4	9.32	<0.0001
Time×site×treatment	8	3.11	0.006

(Fig. 3). Data inspection shows that, in Pick Creek, both planarian and chironomid densities were higher in exclusions than controls and references during salmon spawning, but densities were similar before and after sockeye spawning. However, densities of virtually all other invertebrate taxa at all other sites declined over time, regardless of treatment, indicated by a significant time factor in the various repeated-measures ANOVAs ($P<0.05$) and non-significant time×treatment interactions ($P>0.05$). For example, total invertebrate densities were 10× higher before salmon spawned than after salmon spawned, regardless of treatment, in Hidden Lake Creek (Fig. 3). The exceptions to this pattern were *Gyraulus* snails and Hirundenoidea (leeches) in Lynx Lake, and Bivalvia mollusks and Oligochaeta in Hidden Lake, which did not change significantly over time ($P>0.05$).

The nMDS ordinations and ANOSIMs depict community level differences over time among sites and treatments (Fig. 4). Different sites had different invertebrate assemblages (ANOSIM, Global rho=0.583,$P=0.001$). All pairs of sites were significantly different, with the creeks being the least different (ANOSIM, Global rho=0.15, $P=0.001$), and Pick Creek and Lynx Lake being the most different (ANOSIM, Global rho=0.91,$P=0.001$).

There were differences in composition of the invertebrate assemblage among different time periods in Pick Creek (ANOSIM, Global rho=0.68, $P=0.001$; Fig. 4A), Hidden Lake Creek (ANOSIM, Global rho=0.47, $P=0.001$; Fig. 4B), and Hidden Lake (ANOSIM, Global rho=0.22, $P=0.007$; Fig. 4C). In other words, the composition of the benthic invertebrate communities changed through time in each of these three sites, but more so in the two creek habitats. Disproportionate decreases in densities of the most abundant taxa accounted for most of the observed differences between communities over time (Fig. 3), as indicated by SIMPER analyses. For example, decreases in densities of Tricladida, Siphlonuridae, and Simuliidae (the three biggest contributors to dissimilarity) accounted for 58% of the observed dissimilarity between before and after salmon spawning in Hidden Lake Creek (SIMPER, Fig. 4B). Similarly, in Pick Creek, 50% of the observed dissimilarity between the invertebrate community before and after salmon spawning was due to decreases in Baetid and Siphlonurid mayflies (two biggest contributors to dissimilarity, SIMPER, Fig. 4A). Over 40% of the observed dissimilarity between the invertebrate community before and after spawning in Hidden Lake was due to decreases in chironomid

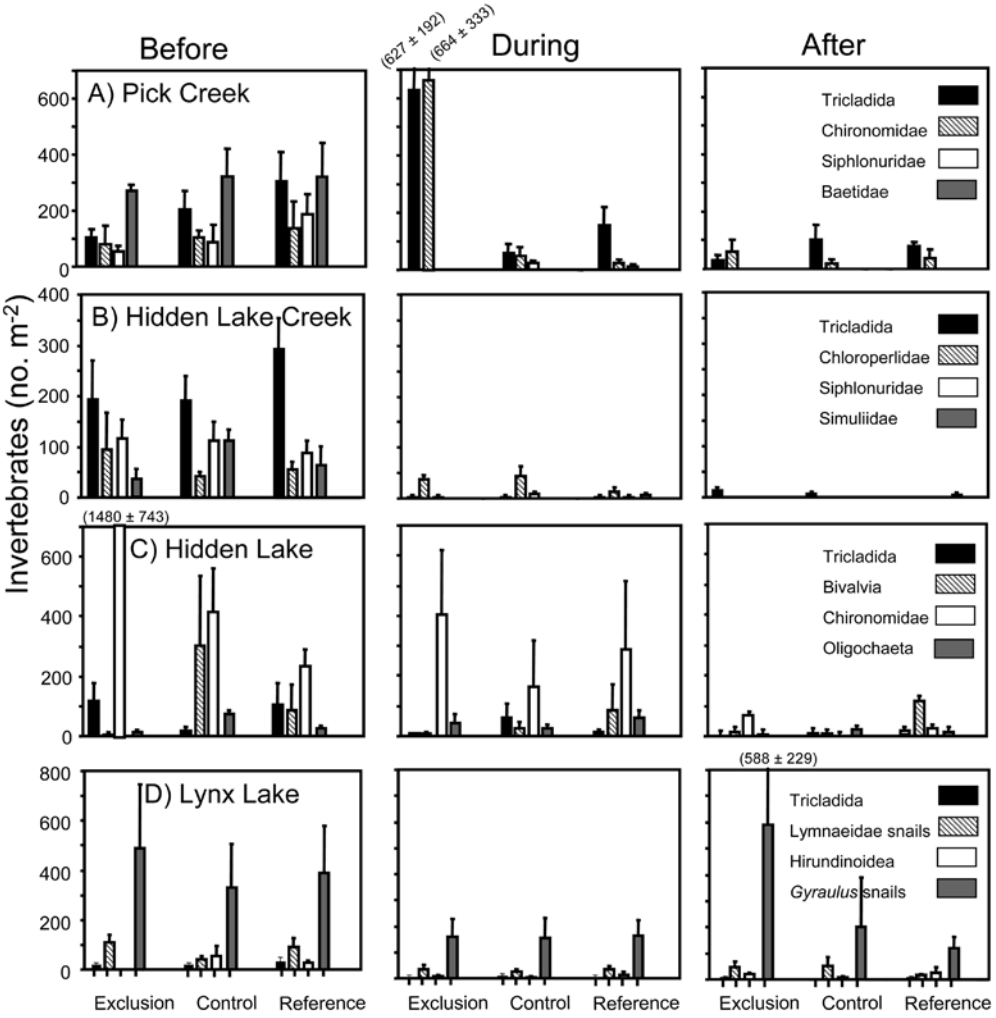

Fig. 3A–D Densities of the four most abundant invertebrates from each site, before, during, and after peak sockeye spawning. Data presented are means±1 SE. Different *shading* of bars represent different invertebrate taxa. Because the four most abundant taxa differed between each site, the four different bar types change from site to site, with the exception of the black bars, which always represent Tricladida. Means or error bars that extended beyond *y*-axes were cut off and are represented by the mean±1 SE in parentheses

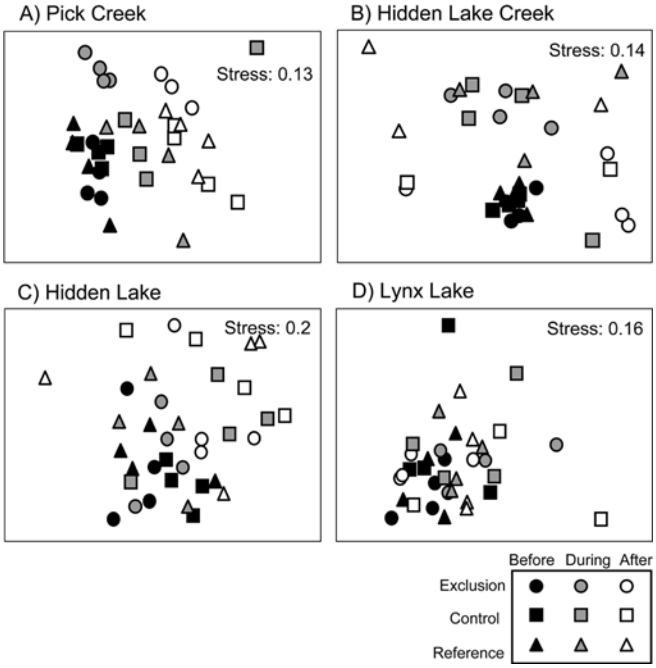

Fig. 4A–D Nonmetric multidimensional scaling ordinations (nMDS) of the invertebrate assemblages for the four study sites. The shading of the symbol indicates the time at which the sample was taken: *black* indicates "before", *gray* indicates "during", and*white* indicates "after" peak salmon spawning. The shape represents the treatment: *circles* represent exclusions, *squares* represent controls, and *triangles* represent references. Each different point represents the pooled invertebrate assemblage from a single plot at a single time. Different sites are shown in different panels. Stress levels represent the ability of the ordination to accurately capture the multidimensional similarity matrix in two dimensions. In nMDS, the relative spacing of the samples on the two-dimensional plane is meaningful, not their position in relation to the arbitrary axes. In the rare case (four of 144 samples) that a sample did not contain any invertebrates, it was excluded from the ordination

abundance (biggest contributor to dissimilarity, SIMPER, Fig. 4C). However, invertebrate assemblages did not differ significantly between dates in Lynx Lake (ANOSIM, Global rho=0.089, $P=0.12$; Fig. 4D).

Treatment did not significantly influence the invertebrate assemblage in three of the four sites either during or after salmon spawning time periods (Fig. 4): Hidden Lake Creek (ANOSIM, $P>0.45$), Hidden Lake (ANOSIM, $P>0.15$), and Lynx Lake (ANOSIM, $P>0.05$). However, there was a significant impact of treatment on invertebrate assemblages in Pick Creek (ANOSIM, Global rho=0.25, $P=0.002$). Exclusion plots were different from both references and controls in Pick Creek during spawning (ANOSIM on "during spawning time" period, Global rho=0.396, $P=0.04$; ANOSIM post-hoc tests, exclusion vs. control, $P=0.029$; exclusion vs. reference, $P=0.029$; Fig. 4A). During salmon spawning, invertebrate assemblages in areas with salmon spawning (references and controls) in Pick Creek were not statistically different (ANOSIM post-hoc test, reference vs. control, $P=0.714$). Post-hoc tests revealed that the invertebrate assemblages in exclusions were significantly different from both the control (ANOSIM, Global rho=0.44,$P=0.002$; Fig. 4A), and reference treatments (ANOSIM, Global rho=0.36, $P=0.001$). The higher densities of Tricladida and Chironomidae in exclusion plots compared to reference and control plots contributed 46% (reference vs. exclusion) and 50% (control vs. exclusion) to the observed differences between treatments during salmon spawning (SIMPER). However, references and controls in Pick Creek had statistically indistinguishable invertebrate assemblages (ANOSIM, Global rho=−0.06, $P=0.72$). These differences between treatments in Pick Creek during salmon spawning was temporary: treatments were not significantly different after salmon spawning (ANOSIM, Global rho=0.137, $P=0.181$).

Discussion

Spawning salmon mobilize fine sediments, which has two main impacts on the local size composition of substrates. First, fine sediments generally decrease in areas where salmon spawn, as previously demonstrated (Kondolf et al. 1993; Montgomery et al. 1996). Second, our experiment demonstrated that fine sediments accumulate in areas where salmon do not spawn, indicated by a relative increase in the proportion of fine sediment in exclusion plots during salmon spawning (Table 1; Fig. 1). Therefore, during spawning, salmon presumably displace fine sediment, which accumulates in areas where salmon do not spawn. For example, in exclusion plots in Pick Creek, fine sediment levels were 5× higher after salmon spawned than before salmon spawned and 5× higher than control and reference plots. Because exclusions accumulated fine sediment displaced by spawning salmon, exclusions do not represent areas totally uninfluenced by salmon. Instead, exclusions are similar to areas undisturbed by direct spawning action adjacent to spawning locations. While these results focused on local displacement and accrual of fine sediment, salmon spawning also mobilizes fine sediment which is then transported downstream and out of the creeks (J.W. Moore, unpublished data). Previous studies have recognized the role of detritivorous fishes and amphipods in reducing the accumulation of fine sediments (e.g., Power 1990; Pringle and Blake 1994; Flecker 1996; Crowl 2001; March et al. 2002). However, no other study, to our knowledge, has described the systematic prevention of fine sediment accumulation by nest-digging fishes.

During nest-digging, salmon can bury or dislodge algae attached to substrates. This periphyton is the base of the benthic food web, directly or indirectly contributing to a variety of invertebrates and fishes (Finlay et al. 2002). In sites with high densities of salmon, areas where salmon spawned had lower levels of algal biomass during spawning than areas where salmon were excluded (Table 2; Fig. 2). Thus, our study experimentally confirms previous observations that periphyton biomass is temporarily lower in salmon spawning locations after salmon spawning (Field-Dodgson 1987; Minakawa and Gara 1999; Peterson and Foote 2000). Although salmon spawning directly decreased algal biomass, it may maintain high levels of primary productivity by displacing fine sediment that can diminish primary production by shading algal substrate (e.g., Power 1990). Therefore, although salmon spawning may decrease periphyton biomass by direct disturbance, they may indirectly increase algal productivity by displacing fine sediment in some systems.

Surprisingly, exclusion of spawning salmon did not have large direct impacts on invertebrate assemblages. Previous research on introduced populations of salmon has suggested that disturbance by spawning salmon can dramatically reduce benthic invertebrate densities (Hildebrand 1971; Field-Dodgson 1987). Minakawa and Gara (2003) observed substantial decreases in invertebrate populations during native chum salmon (*O. keta*) spawning. Peterson and Foote (2000) studied native Alaskan populations of sockeye and observed that some taxa decreased after spawning by salmon. However, if salmon displace invertebrates during nest-digging, then surviving invertebrates would accumulate in areas where salmon did not spawn, including our exclusion plots. Thus, if disturbance by spawning salmon displaced invertebrates, we would predict that after salmon spawned invertebrate densities would increase in the exclusion plots (or at least remain constant) and decrease in the reference and control plots. Consistent with this hypothesis, planaria and chironomid densities increased during salmon spawning in the exclusion plots in Pick Creek (Fig. 3). However, for most taxa and for most sites, we observed that invertebrate densities decreased strongly and similarly in control, reference, and exclusion plots after salmon spawned (Figs. 3, 4). This decrease was strongest in the creek sites—the sites with the highest salmon densities.

There are several possibilities as to why invertebrate densities decreased in entire spawning reaches during salmon spawning, not only in the areas that salmon disturbed directly (Fig. 3). First, it is possible that the lack of a strong treatment effect on benthic invertebrates is because salmon did not disturb the sediments sufficiently in our control plots to cause a difference between areas with and without spawning salmon. However, this hypothesis does not explain the systematic decrease in invertebrate populations as salmon start to spawn. In addition, given that disturbance by spawning salmon strongly impacted sediments and algae, it would be surprising if invertebrates were not also disturbed by the same perturbation. Second, it is possible that densities of benthic invertebrates were too low to identify a treatment effect, perhaps the systematic decrease in invertebrate densities during salmon is simply the natural progression of the benthic invertebrate assemblages, uninfluenced by spawning. Third, it is possible that the impacts of disturbance by spawning salmon are operating on such large temporal and spatial scales that both exclusions and areas with salmon are "disturbed" by spawning salmon. For example, it is possible that densities of aquatic larval insects decrease during salmon spawning because they hatch into terrestrial adults prior to or during salmon spawning. The systematic decrease in invertebrate densities could reflect life-history strategies that are adaptive to past disturbances by spawning salmon. Predictable disturbances can drive evolution of phenology of life-histories (Iwasa and Levin 1995; Lytle 2001). Lytle (1999, 2000, 2002) has demonstrated that aquatic invertebrates with aquatic larval stages and terrestrial adult stages hatch prior to predictable and severe flash flooding. Therefore, we predict that the impact of salmon spawning on invertebrates, and the phenology of insect emergence, would be dependent upon the past disturbance regime that may be strongly regulated by sockeye spawning activities. In other words, disturbance by spawning salmon may have impacted aquatic insects on the evolutionary scale, a scale that is difficult to observe with short-term and small-scale studies such as ours.

Different study sites were impacted differently by spawning sockeye. In general, creek sites had more consistent differences between exclusions and areas where salmon spawned than did the lake sites (Figs. 1, 2, 3, and 4). The different response of lotic versus lentic sites to disturbance by spawning salmon is probably due to a combination of factors. First, by definition, creeks have flowing water which tends to transport suspended materials and organisms unidirectionally downstream. Thus, we would predict that fine sediment or invertebrates that are dislodged into the water column would be displaced farther than if they had been dislodged in a lake. Second, densities of spawning salmon were at least 3× higher in creek sites than lake sites.

This experiment excluded salmon from small areas, even though salmon undoubtedly impact entire ecosystems. Based on our results, we predict that high densities of spawning salmon will temporarily lead to increased fine sediment export, decreased algal biomass, and decreased invertebrate biomass throughout the spawning reach. However, ecosystem-level manipulations of salmon populations are needed to truly isolate the impacts of salmon on coastal ecosystems (Schindler et al. 2003). Studies such as ours will hopefully provide the necessary background for obtaining the substantial political cooperation and funding needed for future ecosystem-level manipulations and other longer-term studies of salmon populations.

Salmon can also have large impacts on freshwater and riparian ecosystems by functioning as vectors of nutrients from marine to coastal ecosystems (Kline et al. 1990; Willson and Halupka 1995; Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). Salmon-derived nutrients are incorporated into a variety of aquatic and terrestrial components of western North America (reviewed by Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). Disturbance by spawning salmon probably influences rates and patterns of uptake of these salmon-derived nutrients. One of the primary pathways by which dissolved salmon-derived nutrients are incorporated into the aquatic ecosystem is through uptake by benthic algae (Schuldt and Hershey 1995; Wipfli et al. 1999). By changing the size distribution of benthic substrate (Kondolf et al. 1993; Fig. 1), salmon modify the surface area available for periphyton. In addition, salmon directly decrease periphyton biomass (Fig. 2), although they may increase periphyton productivity by preventing shading. Therefore, the impacts of salmon-derived nutrients on freshwater habitats may be altered by the disturbance of spawning salmon.

Salmon nest-digging could influence future salmon populations (Schindler et al. 2003). For example, Montgomery et al. (1996) have suggested that by sorting substrate into size-classes during spawning, salmon reduce shear stress and render spawning areas less susceptible to scouring by high flows that could kill incubating eggs and young fish. Alternatively, by reducing fine sediment accrual, spawning salmon may maintain interstitial water and oxygen flow—a necessity for successful egg incubation (Groot and Margolis 1991). As yet, conceptual models of the effects of salmon on ecosystem processes in freshwaters do not embrace the “engineering” effects of healthy salmon populations. Restoration projects on streams and lakes with depressed numbers of salmon have started to use carcasses and fertilizers to replace missing salmon nutrient inputs (e.g., Bilby et al. 1998). Our study demonstrates that the impact of a dead salmon and a live salmon is dramatically different.

The total impact that a species (including habitat modifiers) has on an ecosystem or a community is a function of the per capita interaction strength of that species and its density (Paine 1992; Lawton and Jones 1995). Habitat modifiers often have high impacts on habitats when they reach extremely high abundances that are subsidized by nutrients or energy from outside the area in which they reside (Polis et al. 1997; e.g., Power 1990; Flecker 1996). Anadromous salmon are another example of this: they obtain over 95% of their mass in the ocean and then migrate to their natal stream or lake where they spawn and die, often at very high densities (Marriott 1964; Groot and Margolis 1991). We demonstrate that nest-digging by sockeye can have large impacts on freshwaters, but only in locations with high densities of salmon (e.g., Pick Creek). In areas with few salmon (e.g., Lynx Lake), excluding salmon did not measurably change the benthic community.

One of the largest impacts that humans have had upon freshwaters is the modification of disturbance regimes. Flood suppression has decreased riparian and aquatic productivity (Bayley 1995), facilitated invasion by non-native fish (Fausch et al. 2001), and modified aquatic food web structure (Power et al. 1996; Wootton et al. 1996). However, floods are not the only source of disturbance to freshwaters. Fishes that modify benthic habitat can also impact important ecosystem processes. We have experimentally demonstrated that salmon spawning has profound local impacts on the substrate composition and algal biomass in coastal streams and lake beaches of western Alaska. In the lower 48 states, most populations of salmon have declined dramatically or become extinct in the last century due to anthropogenic impacts such as hatcheries, harvest, blockages of migration pathways, and habitat destruction (NRC 1996; Lichatowich 1999). Thus, by active flood suppression and by depressing populations of anadromous salmon, human impacts have simultaneously reduced two important sources of disturbance to coastal freshwaters of the Pacific Northwest. Globally, human impacts such as fisheries have the potential to remove large amounts of biomass of ecosystem engineers or habitat modifiers from ecosystems (Coleman and Williams 2002). Changing the densities of habitat modifiers, like anadromous salmon, will alter the disturbance regimes of coastal freshwaters, the composition of freshwater communities, and the ecosystem processes they perform.

Acknowledgements This is a contribution from the Alaska Salmon Program at the University of Washington. This work was supported in part by grants from the National Science Foundation, funding from the Bristol Bay salmon processors, as well as fellowships to J.W. Moore from the ARCS foundation, the National Science Foundation, and the department of Zoology at the University of Washington. Jenn Anson, Chris Boatright, Anne Carlson, Brandon Chasco, Tessa Francis, Karen Knirsken, Wendy Palen, and Laura Payne provided critical field or laboratory assistance. Eric Buhle, Stephanie Hampton, Jennifer Ruesink, Amanda Stanley, and two anonymous reviewers provided helpful feedback on earlier drafts of this manuscript.

References

Bayley PB (1995) Understanding large river-floodplain ecosystems. BioScience 45:153–158

Bilby RE, Fransen BR, Bisson PA, Walter JK (1998) Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. Can J Fish Aquat Sci 55:1909–1918

Brenchley GA (1981) Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. J Mar Res 39:767–790

Carpenter S, McCreary NJ (1985) Effects of fish nests on pattern and zonation of submersed macrophytes in a softwater lake. Aquat Bot 22:21–32

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth, UK

Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends Ecol Evol 17:40–44

Crowl TA (2001) Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775–783

Edmunds GFJ, Jensen SL, Berner L (1976) The mayflies of North and Central America. University of Minnesota Press, Minneapolis, USA

Ende CN von (1993) Repeated-measures analysis: growth and other time-dependent measures. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Chapman and Hall, New York, pp 113–137

Fausch KD, Taniguchi Y, Nakano S, Grossman GD, Townsend CR (2001) Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecol Appl 11:1438–1455

Field-Dodgson MS (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

Finlay JC, Khandwala S, Power ME (2002) Spatial scales of carbon flow in a river food web. Ecology 83:1845–1859

Flecker AS (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77:1845–1854

Flecker AS, Taylor BW, Bernhardt ES, Hood JM, Cornwell WK, Cassatt SR, Vanni MJ, Altman NS (2002) Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. Ecology 83:1831–1844

Gende SM, Edwards RT, Willson MF, Wipfli MS (2002) Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928

Gray LJ, Fisher SG (1981) Postflood recolonization pathways of macroinvertebrates in a lowland sonoran desert stream. Am Midl Nat 106:249–257

Groot C, Margolis L (eds) (1991) Pacific salmon life histories. University of British Columbia Press, Vancouver, Canada

Hildebrand SG (1971) The effect of coho spawning on the benthic invertebrates of the Platte River, Benzie County, Michigan. Trans Am Fish Soc 100:61–68

Iwasa Y, Levin SA (1995) The timing of life history events. J Theor Biol 172:33–42

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Kline TCJ, Goering JJ, Mathisen OA, Poe PH, Parker PL (1990) Recycling of elements transported upstream by runs of Pacific salmon: I. 15N and 13C evidence in Sashin Creek, Southeastern Alaska. Can J Fish Aquat Sci 47:136–144

Kondolf GM, Sale MJ, Wolman MG (1993) Modification of fluvial gravel size by spawning salmonids. Water Resour Res 29:2265–2274

Kupriyanova EK, Bailey CF (1998) The disturbance effect of largemouth bass nesting on a benthic macroinvertebrate community. J Freshwater Ecol 13:333–341

Lawton JH, Jones CG (1995) Linking species and ecosystems: organisms as ecosystem engineers. In: Jones CG, Lawton JH (eds) Linking species and ecosystems. Chapman and Hall, New York, pp 141–150

Lichatowich J (1999) Salmon without rivers. Island Press, Washington, D.C.

Loveless CM (1959) A study of the vegetation in the Florida Everglades. Ecology 40:1–9

Lytle DA (1999) Use of rainfall cues by *Abedus herberti* (Hemiptera: Belostomatidae): a mechanism for avoiding flash floods. J Insect Behav 12:1–12

Lytle DA (2000) Biotic and abiotic effects of flash flooding in a montane desert stream. Arch Hydrobiol 150:85–100

Lytle DA (2001) Disturbance regimes and life-history evolution. Am Nat 157:525–536

Lytle DA (2002) Flash floods and aquatic insect life-history evolution: evaluation of multiple models. Ecology 83:370–385

March JG, Pringle CM, Townsend MJ, Wilson AI (2002) Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. Freshwater Biol 47:377–390

Marker AFH, Crowther CA, Gunn RJM (1980) Methanol and acetone as solvents for estimation of chlorophyll a and phaeopigments by spectrophotometry. Arch Hydrobiol 14:52–69

Marriott RA (1964) Stream catalog of the Wood River lake system, Bristol Bay, Alaska. United States Fish and Wildlife Service, Washington, D.C.

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore.

Merritt RW, Cummins KW (eds) (1978) An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa

Minakawa N, Gara RI (1999) Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. J Freshwater Ecol 14:327–335

Minakawa N, Gara RI (2003) Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific Northwest. Trans Am Fish Soc 132:598–604

Montgomery DR, Buffington JM, Peterson NP, Schuett-Hames D, Quinn TP (1996) Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Can J Fish Aquat Sci 53:1061–1070

Myers AC (1977) Sediment processing in a marine subtidal sandy bottom community: I. Physical aspects. J Mar Res 35:609–632

Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269

Naiman RJ, Bilby RE, Schindler DE, Helfield JM (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417

National Research Council (NRC) (1996) Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Paine RT (1992) Food-web analysis through field measurement of per capita interaction strength. Nature 355:73–75

Peckarsky BL, Penton MA (1990) Effects of enclosures on stream microhabitat and invertebrate community structure. J N Am Benthol Soc 9:249–261

Peterson CH (1979) Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston RJ (ed) Ecological processes in coastal and marine systems. Plenum, New York, pp 233–264

Peterson DP, Foote CJ (2000) Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. Trans Am Fish Soc 129:924–934

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

Power ME (1990) Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediments. Ecology 71:897–904

Power ME (1997) Estimating impacts of a dominant detritivore in a neotropical stream. Trends Ecol Evol 12:47–49

Power ME, Parker MS, Wootton JT (1996) Disturbance and food chain length in rivers. In: Polis GA, Winemiller KO (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, New York, pp 286–297

Pringle CM, Blake GA (1994) Quantitative effects of Atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: use of electricity for experimental exclusion. Can J Fish Aquat Sci 51:1443–1450

Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Wayne GW, Reice SR, Sheldon AL, Wallace JB, Wissmar RC (1988) The role of disturbance in stream ecology. J N Am Benthol Soc 7:433–455

Scheffer M, Carpenter S, Foley JA, Foke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Schindler DE, Scheuerell MD, Moore JW, Gende SM, Francis TB, Palen WJ (2003) Pacific salmon and the ecology of coastal ecosystems. Front Ecol Environ 1:31–37

Schuldt JA, Hershey AE (1995) Effect of salmon carcass decomposition on Lake Superior tributary streams. J N Am Benthol Soc 14:259–268

Snodgrass JW, Meffe GK (1998) Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928–942

Statzner B, Fuchs U, Higler LWG (1996) Sand erosion by mobile predaceous stream insects: implications for ecology and hydrology. Water Resour Res 32:2279–2287

Statzner B, Arens MF, Champagne JY, Morel R, Herouin E (1999) Silk-producing stream insects and gravel erosion: significant biological effects on critical shear stress. Water Resour Res 35:3495–3506

Statzner B, Fievet E, Champagne JY, Morel R, Herouin E (2000) Crayfish as geomorphic agents and ecosystem engineers: Biological behavior affects sand and gravel erosion in experimental streams. Limnol Oceanogr 45:1030–1040

Steen RP, Quinn TP (1999) Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. Can J Zool 77:836–841

Stewart KW, Stark BP (1993) Nymphs of North American stonefly genera (Plecoptera). University of North Texas Press, Denton, Texas

Thompson RM, Townsend CR (2003) Impacts of stream food webs of native and exotic forest: an intercontinental comparison. Ecology 84:145–161

Thorp JH (1988) Patches and the responses of lake benthos to sunfish nest-building. Oecologia 76:168–174

Thorp JH, Covich AP (eds) (1991) Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego

Thorp JH, Goldsmith LD, Polgreen JA, Mayer LM (1989) Foraging patterns of nesting and nonnesting sunfish (Centrarchidae: *Lepomis auritus* and *L. gibbosus*). Can J Fish Aquat Sci 46:1342–1346

Wiggins GB (1977) Larvae of the North American caddisfly genera (Tricoptera). University of Toronto Press, Toronto

Willson MF, Halupka KC (1995) Anadromous fish as keystone species in vertebrate communities. Conserv Biol 9:489–497

Wipfli MS, Hudson JP, Chaloner DT, Caouette JP (1999) Influence of salmon spawner densities on stream productivity in Southeast Alaska. Can J Fish Aquat Sci 56:1600–1611

Wootton JT, Parker MS, Power ME (1996) Effects of disturbance on river food webs. Science 273:1558–1561

Zar JH (1999) Biostatistical analysis. Prentice Hall, New Jersey