

Nutrient-dependent recovery of Atlantic salmon streams from a catastrophic flood

Zhongyan Weng, Nandita Mookerji, and Asit Mazumder

Abstract: The impact of a major flood and recovery of the stream communities under contrasting nutrient conditions were studied in two second-order streams of Sainte-Marguerite River, Quebec. A massive flood during the summer of 1996 caused extensive displacement of the stream substratum and severe reductions in the abundance of all biota: periphyton, benthic invertebrates, juvenile Atlantic salmon (*Salmo salar*), and brook trout (*Salvelinus fontinalis*) (especially in the 0+ age-class). In the postflood recovery phase, nutrient-enriched sections recovered significantly more rapidly than the nonenriched sections. After 1 month, periphyton biomass in the enriched sections had increased to five times that of the preflood levels, and after 2 months, the invertebrate communities had recovered to preflood levels. Fish densities and growth rates also returned to normal levels more rapidly in the enriched sections. Our results suggest that nutrient-rich systems are more resilient to massive disturbances, and so, nutrient enrichment may represent a viable tool for restoring nutrient-limited systems.

Résumé : L'impact d'une inondation majeure et le rétablissement subséquent des communautés lotiques dans diverses conditions de nutriments ont pu être étudiés dans deux ruisseaux d'ordre 2 du bassin de la rivière Sainte-Marguerite au Québec. Une inondation massive durant l'été 1996 a causé un important déplacement du substrat des cours d'eau et a réduit de façon significative la densité des organismes, périphyton, invertébrés benthiques, jeunes Saumons de l'Atlantique (*Salmo salar*) et Ombles de fontaine (*Salvelinus fontinalis*), particulièrement ceux de la classe d'âge 0+. Durant la phase de rétablissement après l'inondation, les sections de cours d'eau enrichies de nutriments se sont rétablies significativement plus rapidement que les sections non enrichies. Un mois plus tard, la biomasse du périphyton dans les sections enrichies avait atteint jusqu'à cinq fois la valeur d'avant l'inondation, et après 2 mois, les communautés d'invertébrés étaient retournées aux densités d'avant l'inondation. Les densités et les taux de croissance des poissons ont aussi retrouvé leurs valeurs normales plus rapidement dans les sections enrichies. Nos résultats laissent croire que les systèmes enrichis de nutriments sont plus résistants aux bouleversements massifs et donc que l'addition de nutriments peut s'avérer un outil efficace pour la restauration de systèmes limités par les nutriments.

[Traduit par la Rédaction]

Introduction

It is well known that disturbance, natural or anthropogenic, can affect the structure and function of aquatic and terrestrial ecosystems. However, it is also recognized that ecosystems often show "resistance" and "resilience" to disturbances (Webster et al. 1983; Resh et al. 1988; Biggs et al. 1999). Resistance is the ability of communities or ecosystems to withstand a disturbance, while resilience is the rate of recovery of communities or ecosystems after a disturbance (Biggs et al. 1999). The interactions between these

two components could potentially determine the overall impact of disturbances on ecosystems and their recovery.

The resilience or rate of recovery, which we examine experimentally in this study, is dependent on the severity of the disturbance and its areal extent, availability and characteristics of potential colonists, heterogeneity of the disturbed area, and timing of disturbance (Sousa 1984). In the context of stream restoration, the interest usually lies in understanding how severely affected are the food resources of stream fish communities and predicting how long it may take for the disturbed habitat and the stream communities to return to their "original" condition (e.g., Gore 1985). It is not clearly demonstrated if the recovery of a disturbed food web would be dependent on the availability of nutrients or resources.

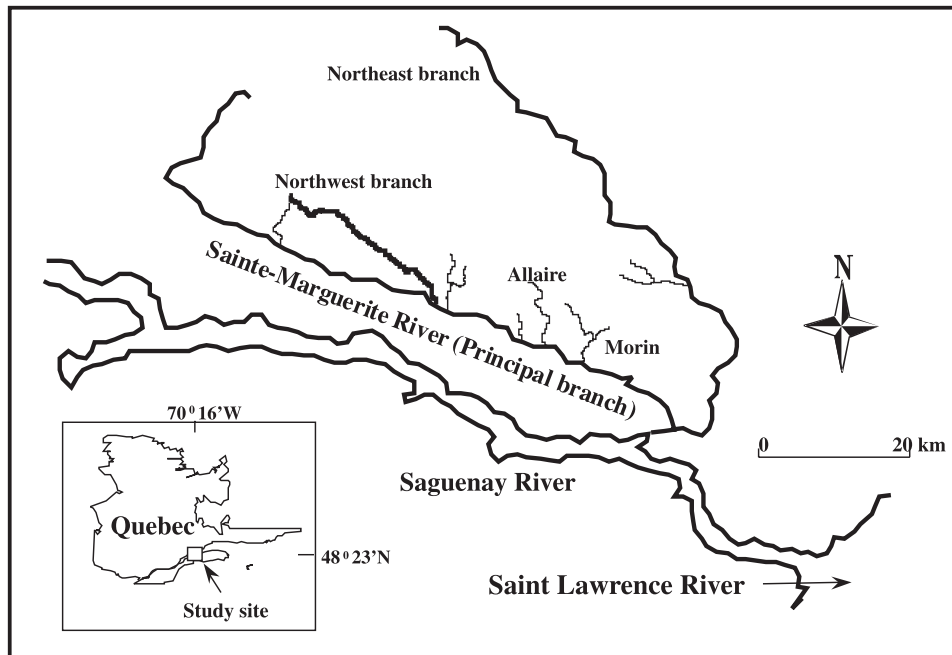
One of the most frequent natural disturbances to stream ecosystems is flooding (Fisher et al. 1982; Michener and Haeuber 1998), but the impact of large-scale floods on natural streams and subsequent recoveries are not well documented (Giller et al. 1991; Michener and Haeuber 1998). Small-scale experiments on flow (e.g., Hooper and Ottey 1988) or substrate disturbance (e.g., Johnson and Vaughn 1995) exist, but they examine only small patches or local events and are unsuitable for studying the impact of floods on a whole stream (Minshall 1988; Giller et al. 1991; Matthaei et al. 1997). Natural "experiments" represent the only viable

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Fig. 1. Study streams (Allaire and Morin) of the Sainte-Marguerite River system, Saguenay region of Quebec.



alternative, as large-scale in situ experiments are logistically quite difficult to conduct.

One such natural experiment occurred in July 1996 while nutrient enrichment experiments were being conducted in an effort to enhance Atlantic salmon (*Salmo salar*) production, when a 100-year catastrophic flood devastated our experiments. This disaster, however, provided us a rare and unique opportunity to examine the influence of enrichment on the recovery of the stream biota. More importantly, the coincidence of the flood with our enrichment experiments allowed us to study the potential mechanisms of how nutrient – food web dynamics could be linked with the recovery of stream communities from a major disturbance.

The first objective of this study was to investigate the impact of the catastrophic flood on periphyton, invertebrate, and fish communities. The second objective was to test the hypothesis that the recovery of stream food webs is dependent on the availability of nutrients. We used 1 year of pre- and postflood data under contrasting enriched versus non-enriched conditions of two streams to test our hypotheses. A similar nutrient enrichment experiment was repeated in 1997, a year without a summer major flood. The 1997 data were used to compare the seasonal patterns for a nonflood year with those for a flood year. Our results will contribute to the understanding of the processes and mechanisms of stream food web recovery and how nutrient enrichment modulates this recovery.

Materials and methods

Experimental sites and the catastrophic flood

This study was conducted in two second-order streams, Allaire and Morin (48°24'N, 70°16'W), flowing into the Sainte-Marguerite River (Fig. 1). The Sainte-Marguerite River, located in the Saguenay region of Quebec, is an important site for the brooders of Atlantic salmon and brook trout (*Salvelinus fontinalis*) and their juveniles.

Historically, this ecosystem supported a flourishing sport fishery for Atlantic salmon. Owing to a drastic worldwide decline in the salmon population during the last decades, commercial and sport fishing have been restricted and Atlantic salmon has been declared an ecologically threatened species (Saunders 1981; Mills 1989). The decline may be related to the low smolt production in the nursery streams, the degradation of spawning and rearing habitats of fish, and the overexploitation in both marine and freshwater environments (Saunders 1981; Mills 1989; Gibson 1993).

Our study streams, Allaire and Morin, varied in width from 4 to 10 m during the summer. Stream substrate was primarily gravel, pebble, and large cobbles, with sand found in small pools. Riparian vegetation along both streams was dominated by red maple (*Acer rubrum*), eastern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), white birch (*Betula papyrifera*), and grasses. The streams received sunlight during most of the day, as trees were generally about 4 m high with around a 12-m gap in forest cover at the sides of the stream channels.

These streams are nutrient poor, as indicated by the concentrations of phosphorus and nitrogen. During the summer base flow period, the concentrations of total phosphorus were relatively stable at around 5 µg·L⁻¹. Total nitrogen concentrations ranged from 150 to 220 µg·L⁻¹. Except during floods, the water seemed to be low in dissolved organic carbon (<6 ppm) and suspended material.

Flood disturbance is generally limited to spring (April–May) in these snowmelt streams. The discharge in summer generally ranged from 0.2 to 1.5 m³·s⁻¹ and during spring floods ranged from 2 to 6 m³·s⁻¹. During July 19–20, 1996, an unusually heavy rainstorm (170 mm within 36 h) produced a 100-year-magnitude flood in the Saguenay region. Besides causing more than \$800 million damage to the local economy and several deaths, this flood resulted in major channel widening, boulder movements, extensive displacement of streambed, and severe erosion and landslides along the Sainte-Marguerite River network (Brooks and Lawrence 1997). In our study area, we recorded a 40-fold increase in stream discharge over the summer base flow (Fig. 2).

Nutrient additions and experimental design

The nutrient enrichment experiments were carried out from June

23 to September 22, 1996. Phosphoric acid was added directly (using a continuous drip system) into the 1-km downstream stretches of both streams to achieve total phosphorus concentrations of approximately $20 \mu\text{g}\cdot\text{L}^{-1}$. The flood occurred during summer when the benthic algal communities were well developed and the salmonid larvae had already emerged. As the flood occurred about 1 month after we started our nutrient enrichment experiments, the enriched and nonenriched sites within both streams were clearly different in nutrients and algal biomass. Due to the high discharge during the flood, the experimental nutrient addition was interrupted for 10 days between July 20 and 29. We restarted our experimental nutrient enrichment immediately after the water level subsided.

The basic experimental design included two similar-sized streams (Allaire and Morin) draining into the same branch of the Sainte-Marguerite River ecosystem (Fig. 1). Each stream had a 1-km upstream nonenriched section and a 1-km downstream enriched section. Within each section, we sampled in 100-m-long stretches for physical (discharge, conductivity, temperature, canopy cover, and current velocity), chemical (different forms of nitrogen and phosphorus), and biological (periphyton, benthic invertebrates, and juvenile salmon and trout) parameters. As we conducted a similar experiment in 1997, a year without a summer catastrophic flood, it was possible to validate our results of flood impacts and recoveries in 1996 with the data from 1997.

Physical and chemical properties

Stream depth was monitored twice every day and converted to discharge (Fig. 2) by constructing a calibration curve from a series of discharge measurements (Gore 1996). Current velocity was estimated with a Pygmy current meter twice every day. Temperature was monitored continuously with a temperature sensor throughout the study period. Conductivity and pH were monitored everyday. Canopy cover was estimated from overhead photographs. A camera was placed horizontally near the stream surface, lens facing up, and an overhead photograph was taken. Canopy cover was then calculated from the percentage covered by the foliage in the photograph.

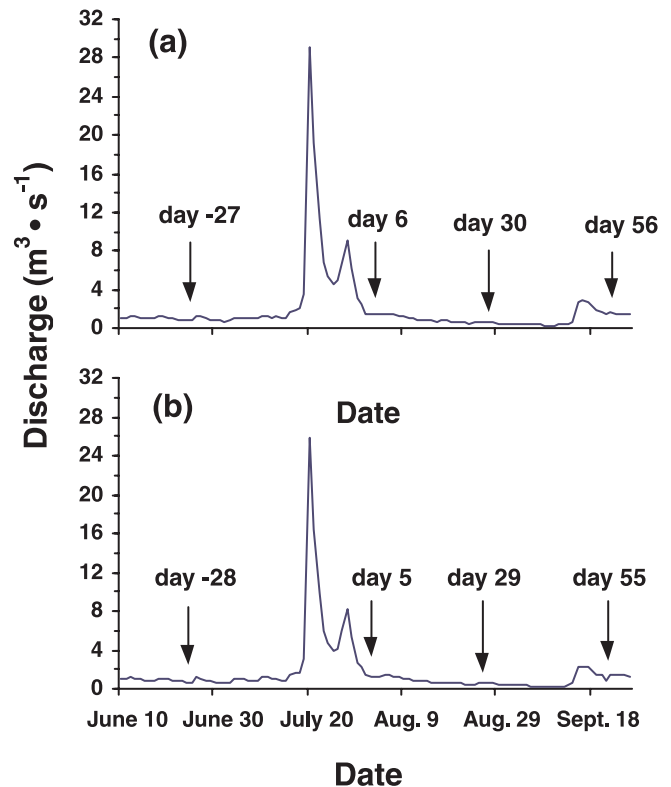
Water samples for chemical analysis were taken weekly at four stations from each of the 1-km upstream nonenriched and 1-km downstream enriched sections. Samples were transported on ice to the field laboratory in <2 h. Total phosphorus was analyzed with the ascorbic acid modification of the molybdenum blue technique (Strickland and Parsons 1972) preceded by potassium persulfate digestion under pressure (Menzel and Corwin 1965). Total nitrogen was determined after wet oxidation with peroxydisulfate digestion (Raimbault and Slawyk 1991). A Technicon autoanalyzer was used for the analyses of nutrients.

Periphyton

Rocks were randomly collected from each of the defined sampling sites. Depth, canopy cover, and current velocity were recorded at each sampling point. To remove the attached algae, each collected rock was thoroughly scraped with a wire brush into a pan containing 1 L of stream water. Six such replicate samples (from six different points within a 100-m sampling site) were collected for periphyton analysis. These samples were placed in dark polyethylene bottles, chilled, returned to the field laboratory, and kept at 4°C . In order to calculate the total surface area of the scraped rocks, the dimensions of each rock were measured with Vernier callipers (Graham et al. 1988). The estimated surface area was used to standardize the periphyton biomass. We considered one third of the total rock surface area as the planar area of stream bottom (Chantha et al. 2000) and expressed periphyton biomass per unit area of the streambed.

The periphyton samples were divided into portions. The subsamples for chlorophyll *a* analysis were filtered through glass-fiber

Fig. 2. Discharge in the (a) Morin and (b) Allaire during summer 1996 and sampling days. A flood occurred during July 20–29, 1996. Days –27 and –28 represent 27 (Morin) and 28 (Allaire) days before the flood. The other days represent the number of days after the flood subsidence.



filters (Whatman GF/C) and frozen in the dark for later analysis. Chlorophyll *a* was measured spectrophotometrically after extraction with 90% boiling ethanol followed by immersion for 24 h at 4°C in the dark and correction for phaeopigments by acidification (Nusch 1980). Subsamples for ash-free dry mass (AFDM) analysis were filtered onto preweighed filters (Whatman GF/C) and dried to a constant weight at 105°C for 24 h. The filters were then ashed at 550°C in a muffle furnace for 4 h and reweighed. The difference in weight before and after incineration was used to calculate the AFDM. AFDM represents all microbial biomass and associated organic material, while chlorophyll *a* represents the autotrophic component (i.e., viable algae).

Benthic invertebrates

Six replicate invertebrate samples were taken with a Surber net (0.0625-m^2 area, $250\text{-}\mu\text{m}$ mesh size) from each of the enriched and nonenriched sections. The rocks were scrubbed and the animals were concentrated into the net. The samples were transferred into plastic jars, chilled, returned to the field laboratory, and deep-frozen at -15°C until analysis. Benthic invertebrates were identified to family, or genus if possible, counted, and measured to the nearest 0.01 mm using a dissecting microscope fitted with an ocular micrometer. The individual invertebrate dry weight was estimated using the length–weight regressions from the literature (Smock 1980; Meyer 1989) and our own site-specific estimates. Using literature information on feeding mode (Merritt and Cummins 1996) and our own observations of gut contents, invertebrates were categorized into dominant functional feeding groups (scrapers, collector–filterers, collector–gatherers, etc.) to allow the analysis of trophic structure.

Table 1. Chemical and physical characteristics in nonenriched and enriched sections of two streams (Morin and Allaire) of the Sainte-Marguerite River.

	Morin		Allaire	
	Nonenriched	Enriched	Nonenriched	Enriched
Total phosphorous ($\mu\text{g}\cdot\text{L}^{-1}$)				
Preenriched period	4.8 (0.5) <i>a</i>	5.1 (0.6) <i>a</i>	4.5 (0.4) <i>a</i>	4.3 (0.4) <i>a</i>
Postenriched period	4.6 (0.6) <i>a</i>	20.2 (3.4) <i>b</i>	4.4 (0.6) <i>a</i>	18.6 (2.7) <i>b</i>
Total nitrogen ($\mu\text{g}\cdot\text{L}^{-1}$)				
Preenriched period	154.1 (16.8) <i>c</i>	158.6 (13.1) <i>c</i>	175.9 (20.7) <i>f</i>	181.3 (15.6) <i>f</i>
Postenriched period	213.9 (18.5) <i>d</i>	176.6 (16.4) <i>e</i>	220.5 (17.2) <i>g</i>	195.7 (21.3) <i>h</i>
pH (entire study period)	6.93 (0.65)	6.59 (0.57)	6.98 (0.56)	6.55 (0.37)
Conductivity (entire study period) ($\mu\text{S}\cdot\text{cm}^{-1}$)	31.9 (2.2)	36.1 (2.5)	29.9 (3.0)	33.2 (3.1)
Temperature (entire study period) ($^{\circ}\text{C}$)	14.9 (0.2) (range 9.9 – 20.2)		14.8 (0.2) (range 10.5–19.6)	
Canopy cover (entire study period) (%)	39.6 (4.7)	45.6 (3.8)	31.3 (4.3)	46.7 (4.8)
Current velocity (nonflood period) ($\text{m}\cdot\text{s}^{-1}$)	0.41 (0.08)	0.36 (0.07)	0.62 (0.14)	0.47 (0.12)

Note: Mean values (\pm SE in parentheses) followed by the same letter are not significantly different (ANOVA: $P > 0.05$).

Fish

Fish densities were determined by electrofishing using population depletion estimates in both enriched and nonenriched sections (Li and Li 1996). Fish were collected during June 15–18, July 16–19, and August 24–26, 1996, and June 22–24, July 25–27, and August 21–24, 1997, and released alive after recording length and weight. Age distribution of fish was determined by using growth rings from otoliths of around 10 fish for each size-class.

Statistical analyses

To test the significance of flood impact, we used one-way analysis of variance (ANOVA) comparing the data for pre-flood (day –27) and post-flood (day 5) dates. One-way ANOVA was also used to test the impact of enrichment (two levels, enriched versus nonenriched) on different indicator variables for four individual dates. Second-order polynomial regressions were used to determine the recovery patterns for periphyton and invertebrates. In the regression equations, the positive linear coefficients indicated the biomass and density accruals during the recovery period, while the negative quadratic coefficients indicated the population decline during the later phase of the recovery period. We also used one-way repeated measures ANOVA to validate the significance of recovery in chlorophyll *a* by using nutrient enrichment as a main factor. Systat version 8 was used for all of the statistical analyses.

Results

Physical and chemical properties

At the start of the experiment, the differences in the total phosphorus concentrations between the nonenriched and enriched sections for each stream were statistically insignificant (ANOVA: Morin, $P = 0.52$; Allaire, $P = 0.39$) (Table 1). During the course of the enrichment, the total phosphorus concentrations in the enriched sections were nearly four times higher than those in the nonenriched sections of both Morin and Allaire (Table 1). During the postenriched period, the total nitrogen concentrations were 213.9 and 220.5 $\mu\text{g}\cdot\text{L}^{-1}$ in the nonenriched sections of Morin and Allaire, respectively, while they were 176.6 and 195.7 $\mu\text{g}\cdot\text{L}^{-1}$, respectively, in the enriched sections (Table 1). The significantly lower (ANOVA: Morin, $P = 0.027$; Allaire, $P = 0.036$) total nitrogen concentrations in the enriched sections could have been due to a greater uptake by benthic algae and bacteria. The other chemical and physical characteristics (pH, conductivity, tempera-

ture, canopy cover, and current velocity) were similar in the nonenriched and enriched sections of the two streams during the entire study period (Table 1).

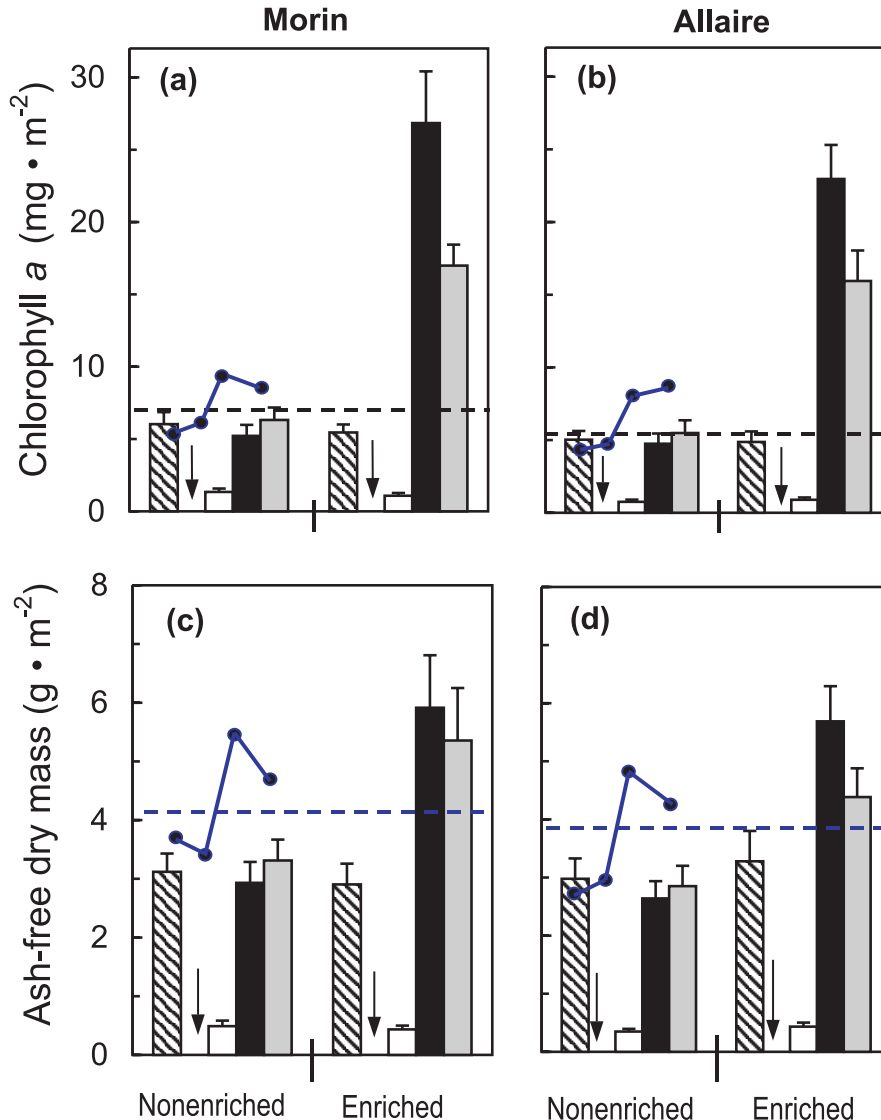
Periphyton

The periphyton (algae and associated organisms on rocks) biomass, as indicated by chlorophyll *a* concentrations and AFDM, was significantly reduced by the flood (one-way ANOVA using pre- and postflood data: $P < 0.001$). The average chlorophyll *a* concentrations dropped from the pre-flood levels of 5.7 and 4.9 $\text{mg}\cdot\text{m}^{-2}$ to postflood levels of 1.2 and 0.8 $\text{mg}\cdot\text{m}^{-2}$ in Morin and Allaire, respectively (ANOVA, $P < 0.001$) (Fig. 3). Similarly, the AFDM declined by more than 85% at all sites ($P < 0.001$) (Fig. 3). In comparison, during the same time period in July of 1997, a year without a flash flood, the chlorophyll *a* concentration and AFDM remained at around 6 $\text{mg}\cdot\text{m}^{-2}$ and 4 $\text{g}\cdot\text{m}^{-2}$, respectively (Fig. 3, second data points on solid lines). After the flood, periphyton biomass returned to its usual seasonal average levels (e.g., Fig. 3, 1997, broken lines) in both nonenriched and enriched sections. However, 1 month after the flood, chlorophyll *a* and AFDM in the enriched sections of both streams increased to fivefold and twofold of those in the nonenriched sections, respectively (Fig. 3, solid bars). By day 55–56, chlorophyll *a* levels exceeded 16 $\text{mg}\cdot\text{m}^{-2}$ in the enriched sections, while chlorophyll *a* levels in the nonenriched sections were around 5 $\text{mg}\cdot\text{m}^{-2}$ (repeated measures ANOVA: $P < 0.001$) (Figs. 3a and 3b, gray bars).

Benthic invertebrates

The flood caused 87–93% declines in the density of invertebrates from the pre-flood levels (around 5200 individuals $\cdot\text{m}^{-2}$ in June 1996; one-way ANOVA: $P < 0.001$) (Fig. 4). In late July, the density of invertebrates usually remained at around 4500 individuals $\cdot\text{m}^{-2}$ (Fig. 4, second data points on solid lines). The biomass of invertebrates showed similar impacts of flood in the nonenriched and enriched sections (ANOVA: $P > 0.05$). Following the flood, the biomass of invertebrates dropped from 600 to <50 $\text{mg}\cdot\text{m}^{-2}$ at all sites (ANOVA: $P < 0.001$) (Fig. 4). In the nonenriched sections of both streams, the invertebrate communities recovered only up to 30% of their seasonal average levels (e.g., Fig. 4, 1997, broken

Fig. 3. Periphyton biomass, (a and b) chlorophyll *a* and (c and d) AFDM, in the Morin and Allaire under nonenriched and enriched conditions. Arrows indicate the occurrence of the flood during July 20–29, 1996. Histograms indicate the mean values ± 1 SE ($n = 6$) on four sampling occasions in 1996: 27–28 days before the flood (hatched bars), 5–6 days after the flood (open bars), 29–30 days after the flood (solid bars), and 55–56 days after the flood (gray bars). The broken lines represent the seasonal averages under nonenriched conditions during a nonflood year (1997, $n = 40$). The solid lines represent the summer seasonal pattern under nonenriched conditions in 1997 (each point is a mean of 10 observations).



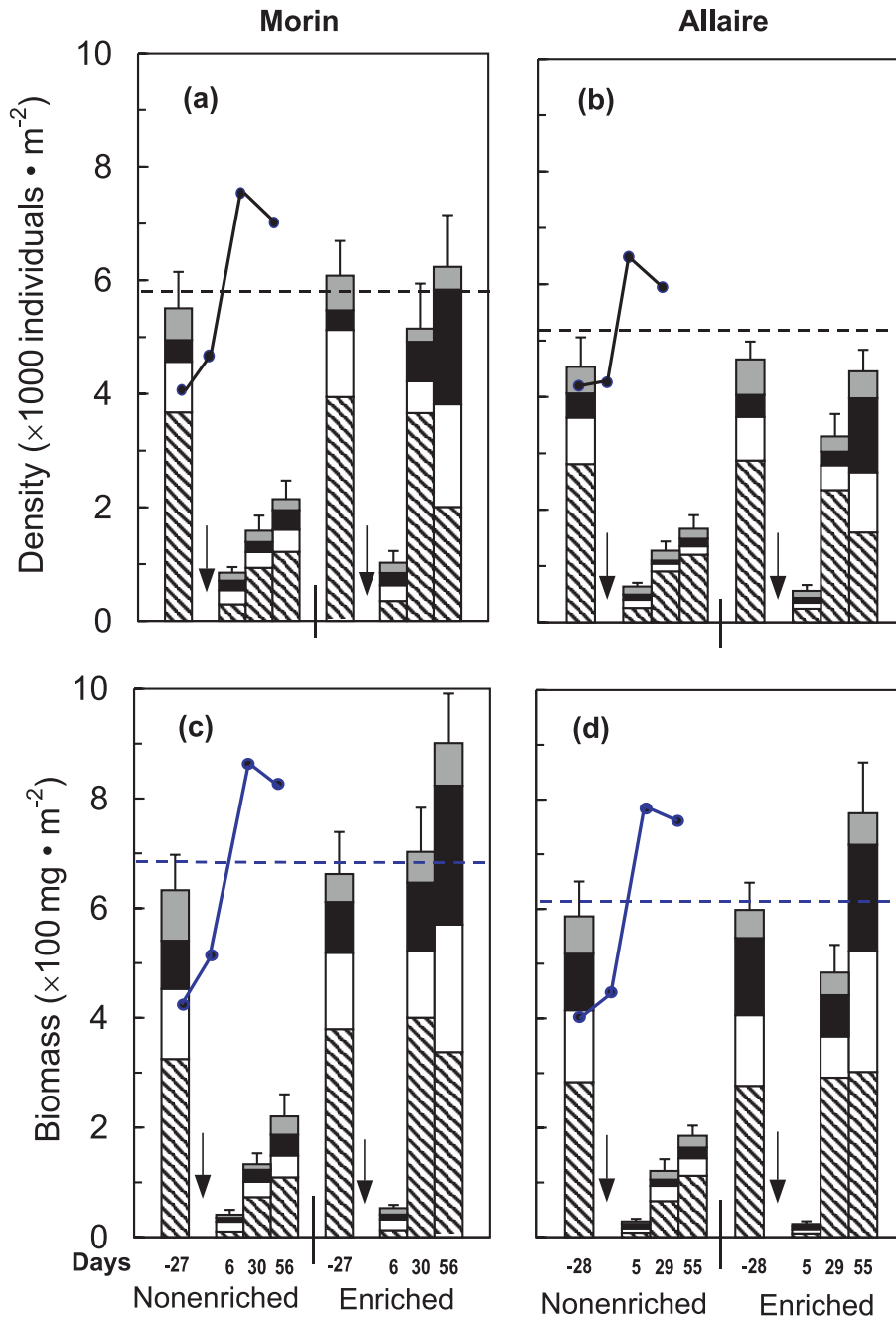
lines) even 55 days after the flood. On the other hand, in the enriched sections, both the density and biomass of invertebrates reached 80–100% of their seasonal levels within only 30 days after the flood ($P < 0.001$) (Fig. 4). This recovery of invertebrates in the enriched sections was mainly due to the increases in the groups of insects that feed primarily on periphyton (Fig. 4). These functional feeding groups were collector–gatherers (mainly mayfly nymphs of Baetidae and Ephemeroptera and midge larvae of Orthocladinae), scrapers (mainly mayfly nymphs of Heptageniidae), and collector–filterers (caddisflies of Philopotamidae and Hydropsychidae and blackflies of Simuliidae). After 55 days following the flood, the largest increase in density and biomass of invertebrates in the enriched sections was due to two groups, the

scrapers and the collector–filterers (Fig. 4). This pattern was consistent for the enriched sections of both streams.

Atlantic salmon and brook trout

During the preflood period, the densities of juvenile Atlantic salmon were on an average 20 and 11 individuals $\cdot 100 \text{ m}^{-2}$ in Morin and Allaire, respectively, while the average densities of brook trout were 5 and 13 individuals $\cdot 100 \text{ m}^{-2}$, respectively (Fig. 5, 1996). Immediately after the flood, fish abundance was very low throughout the two streams. One week after the flood, upstream movement of the surviving fish from the principal branch started to reestablish the population of both Atlantic salmon and brook trout in the streams. One month after the flood, the densities (average of all sampling

Fig. 4. (a and b) Densities and (c and d) biomass of benthic invertebrates in the Morin and Allaire under nonenriched and enriched conditions. Histograms indicate the mean values ± 1 SE ($n = 6$) for the total density and biomass of benthic invertebrates. Different shading in each histogram shows the contributions of various invertebrate functional feeding groups to the total density and biomass: hatched, collector-gatherers; open, collector-filterers; solid, scrapers; gray, other functional groups. Arrows indicate the occurrence of the flood during July 20–29, 1996. The broken lines represent the seasonal averages under nonenriched conditions during a nonflood year (1997, $n = 40$). The solid lines represent the summer seasonal pattern under nonenriched conditions in 1997 (each point is a mean of 10 observations). Days –27 and –28 represent 27 (Morin) and 28 (Allaire) days before the flood. The other days represent the number of days after the flood subsidence.



sites) returned to 76 and 56% of the preflood densities for salmon and trout, respectively (Fig. 5, 1996). A severe loss in density was seen in the 0+ age-class (Fig. 5, August 1996), and consequently, in the following year (1997), this was reflected in the relatively low density of the 1+ age-class for both salmonid species (Fig. 5, 1997). The recovery

in the densities of 1+ and 2+ salmonids was distinctly better in the enriched sections (Fig. 5, August 1996). Furthermore, the weight gains of 1+ and 2+ salmonids were faster in the enriched sections than in the nonenriched sections (Table 2). By the end of August (1 month after the flood), the fish from the 1+ and 2+ age-classes were significantly heavier in

Fig. 5. Average total densities of (a–d) Atlantic salmon and (e–h) brook trout from two sampling sites of nonenriched and enriched sections in the Morin and Allaire in 1996 and 1997. Different shading in each histogram shows the contributions of various age-classes to the total density: solid, 0+ age-class; open, 1+ age-class; gray, 2+ age-class. Arrows indicate the occurrence of the flood during July 20–29, 1996.

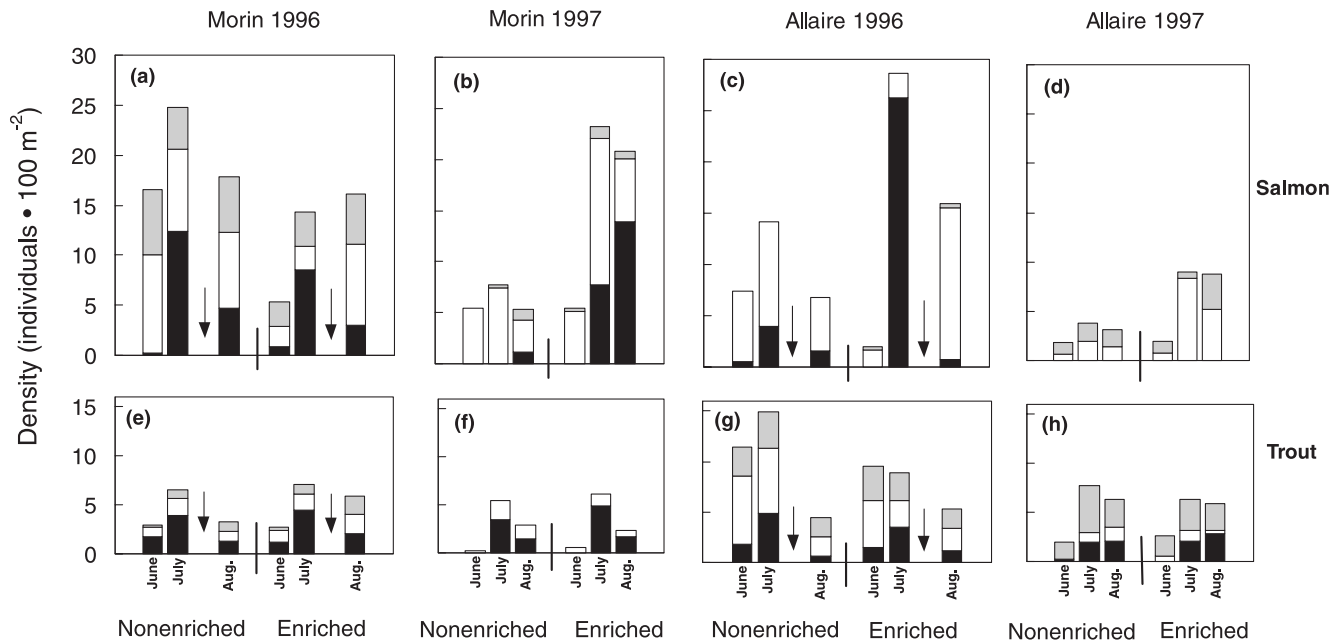


Table 2. Mean wet weights (g) (± 1 SE in parentheses) of Atlantic salmon and brook trout captured in nonenriched and enriched sections of two streams (Morin and Allaire) of the Sainte-Marguerite River during August 24–26, 1996.

	Morin		Allaire	
	Nonenriched	Enriched	Nonenriched	Enriched
0+ Atlantic salmon	1.50 (0.09)	1.46 (0.07)	1.53 (0.09)	1.63 (0.19)
1+ Atlantic salmon	5.92 (0.35)	7.87 (0.56)	8.20 (0.68)	9.79 (0.36)
2+ Atlantic salmon	13.19 (0.61)	17.20 (1.59)	na	20.51 (2.87)
0+ brook trout	1.93 (0.38)	2.46 (0.32)	2.27 (0.11)	1.86 (0.12)
1+ brook trout	10.57 (1.49)	13.04 (2.04)	9.78 (0.58)	13.36 (1.10)
2+ brook trout	21.89 (2.93)	29.64 (5.18)	27.63 (3.62)	35.06 (4.57)

Note: na, not available.

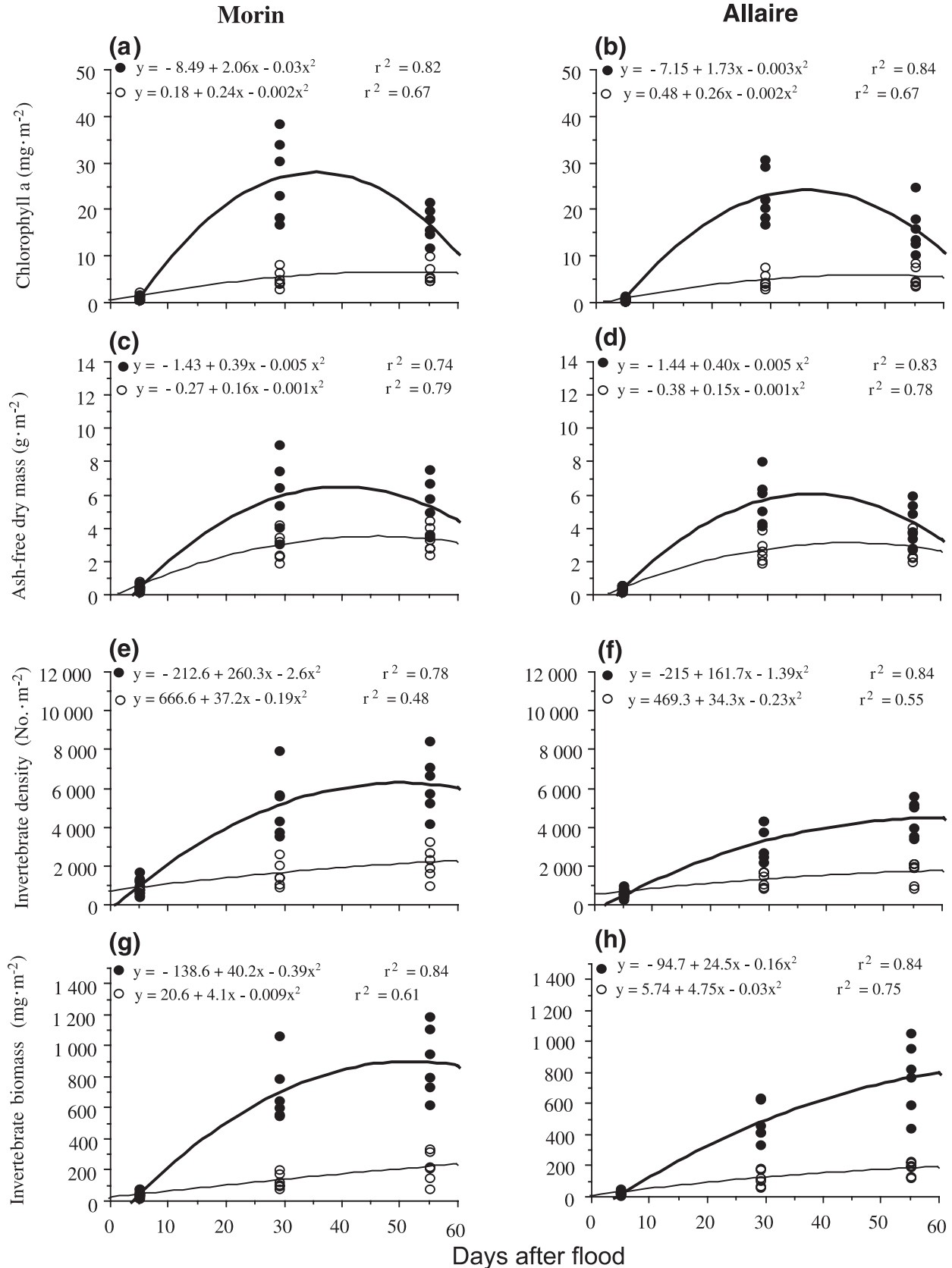
the enriched sections than those in the nonenriched sections (Student's *t* test: $P < 0.01$). The mean weights of 1+ and 2+ salmon in the enriched sites were 19–33 and 30% higher, respectively, than those in the nonenriched sites. The 1+ and 2+ trout were 23–37 and 27–35% heavier, respectively, in the enriched sections than those in the nonenriched sections (Table 2).

Patterns of recovery

Based on the second-order polynomial regression analyses of chlorophyll *a*, AFDM, and the density and biomass of invertebrates as a function of days following flood, we were able to quantify the patterns of recovery by each of these food web components (Fig. 6). As indicated by the linear coefficients of the regression equations, the periphyton recovered at significantly higher rates of 1.73–2.06 mg chlorophyll *a*·m⁻²·day⁻¹ in the enriched sections of Allaire and Morin compared with 0.24–0.26 mg chlorophyll *a*·m⁻²·day⁻¹

in the nonenriched sections of both streams. However, due to the intensive grazing activities in the enriched sections of both streams, the concentrations of chlorophyll *a* declined after postflood day 35, as indicated by the negative quadratic coefficients of the regression equations. AFDM, an indicator of both the auto- and heterotrophic components of periphyton biomass, showed similar patterns of recovery. However, there is a greater overlap of data points for AFDM between enriched and nonenriched sections. We think that this overlap may be due to the contribution of the heterotrophic components of periphyton, which may not have responded as positively as the autotrophic components (chlorophyll *a* from viable algae). Invertebrate density increased at rates of 161–260 individuals·m⁻²·day⁻¹ in the enriched sections of Allaire and Morin compared with 34–37 individuals·m⁻²·day⁻¹ in the nonenriched sections. The invertebrate community also showed six to eight times faster biomass accumulation (24–40 mg dry weight·m⁻²·day⁻¹) in the enriched sections than in the

Fig. 6. Polynomial regressions of periphyton biomass, (a and b) chlorophyll a and (c and d) AFDM, and invertebrate (e and f) density and (g and h) biomass against days after the flood in the Morin and Allaire in 1996. Solid circles and thick lines represent data and regressions for enriched sections, and open circles and thin lines represent data and regressions for nonenriched sections.



nonenriched sections ($4\text{--}5 \text{ mg dry weight}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) of both streams (Fig. 6).

Discussion

The structure and functioning of stream ecosystems depend on the water flow patterns, availability of suitable habitat for colonization by stream biota, and the flow patterns of matter and energy along the food webs (Allan 1995). Our study suggests that a potential impact of major floods on the structure and functioning of stream ecosystems is associated with the disruption of nutrient and food web dynamics. Specifically, we demonstrate that the availability of nutrients and the resources for higher trophic levels are important determinants of the recovery of stream ecosystems from flood damage.

The time required for disturbed stream communities to recover varies widely from a few days to several months or even years (Niemi et al. 1990). Earlier studies suggested that the rate of recovery may be largely related to the severity of the flood events and the dependence on the local environmental conditions. For example, Sousa (1984) suggested that the recovery of streams depends on the magnitude and timing of the disturbance, heterogeneity of the disturbed area, and the attributes of colonists. Steinman and McIntire (1990) concluded that the recovery of periphyton after a flood depends on periphyton propagule abundance, propagule composition, and local environmental conditions (i.e., current velocity, light, nutrients, herbivory, etc.). The importance of nutrients and light for the recovery of periphyton from scouring damage has been suggested by Biggs et al. (1999) based on the results from experimental streams. Their study showed that nutrients were the most important regulator of resilience. In their experiment, periphyton under a high availability of nutrients recovered faster than periphyton under low nutrient availability. The uniqueness of our study is the integration of all of the dominant trophic linkages and their interdependence during the recovery from a major natural flood in stream ecosystems. In our study, the observed patterns of contrasting recovery of the stream food web in enriched versus nonenriched sections clearly indicate the dependence of higher trophic levels on the recovery of lower trophic levels and the associated availability of nutrients. We show that nutrient-poor streams take a significantly longer time to recover and function normally after a major disturbance. The invertebrate and fish communities did not recover in the nutrient-poor condition even 2 months after the flood. This delayed recovery from flood damage may have major implications for juvenile fish recruitment and productivity in oligotrophic nursery streams.

Nutrients, light, temperature, current velocity, and grazing pressure have been suggested to regulate periphyton biomass (Steinman and McIntire 1990; Biggs et al. 1999; Rosemond et al. 2000). Periphyton is the major food source of over 80% of the insect communities in our stream ecosystems, and these insects are the primary food of juvenile salmon and trout (Merritt and Cummins 1996; Mookerji et al. 1998). Being the lowest trophic level, periphyton showed a faster response to nutrient additions than the higher trophic levels. The additional nutrient resources in the enriched sections strongly stimulated growth rates and biomass accrual, which

caused faster recovery. It is unlikely that our stream sites are light-limited, as the canopy cover on an average was 31–47% in both streams. Abundant light and continuously high temperature during the postflood period in summer may also have contributed to this rapid recovery, as also observed by Fisher et al. (1982) for Sycamore Creek, Arizona. The physical characteristics of the streams are similar in both enriched and nonenriched sections. Thus, our results suggest that the contrasting recovery patterns of periphyton and higher trophic levels are due mostly to the enhanced availability of nutrients. Steinman et al. (1991) and Mulholland et al. (1991) reported that nutrients enhance periphyton regeneration rates following light elimination and scour disturbance in laboratory streams. Valett et al. (1994) have noted the importance of nutrients for the recovery of a Sonoran desert stream from flood disturbance. The present study is likely the first in situ experiment directly demonstrating the dependence of all major trophic levels on the availability of nutrients following a massive flood.

Wallace (1990) pointed out the following mechanisms of recolonization associated with the recovery of stream benthic invertebrates from a disturbance: (i) migration from the deeper hyporheic zone to surface substrates, (ii) upstream movements, (iii) downstream drift from upstream or tributary areas, and (iv) aerial recolonization by adults. In our study, the presence of unhatched eggs as well as ovipositing adult insects during the midsummer and the migration from the hyporheic refugia soon after the flood represent the most likely recolonization processes. This is because the impact of the flood was similar throughout the streams, and thus, neither upstream nor downstream movement of invertebrates was the major mechanism for the rapid recovery. In our streams, most of the insects (e.g., mayflies and midges) typically have short generation times and various life history patterns (Niemi et al. 1990; Wallace 1990). Hence, they could rapidly increase their abundance following the enhancement of their food resources (periphyton) in the nutrient-enriched sections.

Soon after the flood, upstream movement of the fish from the connecting main river restored the fish populations in the two streams. The densities of the 1+ and 2+ age-classes for both salmon and trout reestablished relatively quickly in the nutrient-enriched sections. However, the 0+ age-class salmonids suffered more than the larger age-classes (1+ and 2+), as indicated by the very low density of the 1+ age-class in the following year (1997). Based on this observation, we are expecting a low adult return of the 1996 year-class of salmon in 2000 and 2001. As the trophic linkages were disrupted by the flood, the fish communities could not recover under nutrient-poor conditions. Thus, it seems that nutrient-poor streams and rivers can potentially lose single or multiple year-classes of fish because of the slow recovery of the lower trophic levels. On the other hand, the experimental nutrient additions that triggered a faster recovery of the periphyton produced an increased high-quality food base for the rapid increase of the major insect groups, the grazers. Since the grazing insects (mainly mayflies) are the preferred food of salmonids in our streams (Mookerji et al. 1998), we observed a higher growth of fish in the enriched sections.

In conclusion, our results show that major flood events can severely reduce the populations of stream biota and that

nutrient-poor streams take longer to recover from such flood impacts. However, an additional source of nutrients could speed up the recovery process. We demonstrate experimentally that the recovery rates of higher trophic levels are strongly dependent on the availability of nutrients and associated recovery of periphyton. A large number of nursery streams of juvenile salmonids are often nutrient poor or oligotrophic (Gibson 1993; Allan 1995) and therefore could be highly vulnerable to episodic floods. We suggest that appropriately controlled nutrient addition could be effective in restoring the food webs and fisheries of nutrient-poor ecosystems following large floods.

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