

ORIGINAL PAPER

Margaret A. Palmer · Peter Arensburger
Andy P. Martin · Daniel W. Denman

Disturbance and patch-specific responses: the interactive effects of woody debris and floods on lotic invertebrates

Received: 6 February 1995 / Accepted: 22 July 1995

Abstract Disturbance may play an important role in generating patterns of abundance and distribution of biotic assemblages, particularly if its impact differs among habitat patches. Despite much speculation concerning the probable importance of spatial variation in the response of stream fauna to flooding, empirical work on patch-specific responses to spates is largely lacking. Floods typically reduce the abundance of lotic invertebrates dramatically in open-channel areas. We conducted a set of experiments to determine if faunal abundances are less affected in patches more sheltered due to the presence of woody debris dams. Specifically, we tested two hypotheses using chironomids and copepods living in a warmwater, 4th order stream: (1) the effect of flooding on the fauna varies between patches associated with debris dams versus the open channel, and (2) the absence of woody debris in a stream impedes faunal recovery throughout the channel following floods. We tested the first hypothesis by quantifying faunal abundances prior to, during, and following two floods in four patch types: mid-channel sandy patches distant from dams, coarse sediments associated with dams, fine sediments associated with dams, and leafy debris in dams. The second hypothesis was tested by removing all of the woody debris from two stretches of the stream and comparing the impact of a flood on fauna in debris-removed versus control stretches. Across all of the eight study dams, there were patch-specific faunal responses to two floods. Removal of woody debris from the stream did not prevent faunal recovery throughout the channel; however, the presence

of woody debris dams did confer greater resistance of fauna to floods (as measured by no decrease in abundance during flooding) in two patch types. Abundances of chironomids and, to a lesser extent, copepods in the leafy debris of dams and in fine sediment patches associated with some dams either did not change or increased during floods, despite the fact that abundances in the dominant patch type of the stream (the sandy mid-channel) were reduced by 75–95%. All instances of faunal increase were limited to fine sediment patches associated with dams, thus entire dams cannot be labeled as flow refugia per se. Statistically, we distinguished fine patches which accumulated animals during floods from the other fine patches based on two physical attributes. Patches accumulating animals were all characterized by low water flux and near-bed flow, which likely contributed to the retention and/or passive deposition of animals. Whole dam attributes (e.g. dam size or complexity) were not useful in predicting which of the dams would accumulate animals in their fine sediments during flooding. Although structural complexity – here in the form of wood and leafy debris – is clearly important in generating biotic pattern in many ecosystems, our work underscores the need to understand what processes are responsible for the link between physical structure and biotic pattern.

Key words Disturbance · Patchy environments · Floods · Woody debris · Lotic invertebrates

Introduction

Increasingly, ecologists are recognizing that linking biological patterns to their underlying processes often requires knowledge of spatial variation in those processes. Physical and biological disturbance plays a dominant role in generating patterns of abundance and distribution for a variety of plant and animal assem-

M. A. Palmer (✉) · P. Arensburger · A. P. Martin
Department of Zoology, University of Maryland,
College Park, MD 20742, USA

D. W. Denman
Statistics Laboratory, Computer Science Center,
University of Maryland,
College Park, MD 20742, USA

blages (Paine 1966; Sousa 1984). The magnitude and impact of a disturbance varies spatially in many systems (Pickett and White 1985; Turner 1987). Indeed, differences in the response of local populations to disturbance may allow persistence regionally, despite unstable local fluctuations and extinctions (e.g. DeAngelis and Waterhouse 1987). If the impact of disturbance differs among habitat patches, then the abundance and spatial arrangement of patches, as well as dispersal capabilities of the fauna, may determine population resilience in an ecosystem.

In lotic environments, floods are a dominant disturbance often occurring unpredictably and with sufficient severity to essentially reset communities (Boulton et al. 1992; Resh et al. 1988). Floods occur over broad spatial scales that often include many patch types which may be influenced to differing degrees by flow disturbances (Marmonier and Creuzé de Châtelliers 1991; Pringle et al. 1988). A variety of stream patches have been suggested as potential refugia, the persistence and connectivity of which may be critical to the survival of lotic fauna (Hildrew et al. 1991; Sedell et al. 1990), but empirical work on patch-specific faunal responses to individual spates is largely lacking.

Our past work in a warmwater, sandy-bottomed stream (Palmer et al. 1992) documents a pattern typical of many streams worldwide: dramatic reductions in the abundance of invertebrates during flooding (Hildrew and Giller 1994; Resh et al. 1988). Our work was completed in the dominant patch "type" for our stream – the sandy mid-channel. Here, we report on a set of experiments designed to determine if faunal abundances in patches that are potentially sheltered by woody debris are less impacted by floods. We tested two specific hypotheses: (1) the effect of flooding on stream fauna varies between patches associated with dams versus the open channel, and (2) the absence of woody debris from a stream will impede faunal recovery throughout the channel following floods. The motivation to focus on debris dams included: work suggesting, but not demonstrating, that dams do offer refugia for stream animals during floods (Borchardt 1993; Lancaster and Hildrew 1993); evidence that woody debris enhances the (passive) retention of organic matter in streams (Bilby 1981; Bretschko 1990; Naiman 1982) and the possibility that the high faunal abundances often found in debris dams (Smock et al. 1989; Wallace and Benke 1984; Winkler 1991) result in part, from flow effects.

To examine patch-specific responses to flooding, we focused primarily on copepods and larval chironomids. These are two of the most abundant invertebrate taxa in our study stream and they are numerous over spatial scales that incorporate a myriad of patch types (Poff et al. 1993). Past studies on the transport and settlement dynamics of these fauna (Palmer 1992) have shown that increased flow leads to their passive entry

into the water column and that, for the most part, these animals act like passive particles in stream flow. This means that structural features that alter hydrodynamics, like woody debris, are likely to influence erosion and settlement of these small animals. Thus, the impact of floods on copepods and chironomids may be mitigated by debris dams by reducing passive displacement or enhancing deposition of these fauna (both processes are probably related to mortality) relative to open channel areas.

Because we wished to embrace the real world complexity of dams, we tested our hypotheses in the field, rather than in a simplified laboratory setting, or using simplified, artificially built dams. In nature, no two debris dams are alike, and a single dam can create both erosional and depositional effects. Our goal was to determine if these complex, natural debris dams influenced the impact of flood disturbances on benthic faunal abundances, fully expecting that biotic patterns might differ among dams. Empirical field studies such as these are necessary to understand how physical heterogeneity and disturbance interact to influence biotic patterns.

Materials and methods

Study site

Goose Creek is a low-gradient, 4th order stream in northern Virginia. It has year-round flow, a width of ≈ 20 m and mean annual discharge of ≈ 8.5 m³/s. The stream is fairly simple geomorphologically, with long, straight stretches of sandy bottom and occasional short riffles of gravel, cobbles, and sand (detailed description in Palmer 1992). Debris dams of varying size and architecture are common along the margins of the channel (Table 1). Two dams in each of four 100-m stretches of the stream were chosen for study (Fig. 1). Stretches were at least 100 m apart to minimize effects of faunal dispersal between stretches. The dispersal distance for the Goose Creek copepods and chironomids is short (1–5 m) at low to moderate flows (Berger 1994; Palmer 1992), but unknown during floods. The hydrodynamic effects of individual dams did not overlap (i.e. were independent), as determined by flow visualization studies (see below).

Dominant patch types were identified in a preliminary survey, carried out over several dates, of flow and granulometry around each dam. Depositional areas were termed *fine patches* because they generally experience low flow and are dominated by fine sediments of silt and clay. The erosional areas were termed *coarse patches* since they experience higher flows and have a poorly sorted substrate of sand, pebbles, and some cobble. Leafy materials within each dam were termed *debris patches*. Finally, we identified *mid-channel* sampling areas (well-sorted sands) lateral to each dam that were free of hydrodynamic influences of the dams. These areas were determined by injecting dye upstream of the dams under various flow conditions and observing flow pathlines. We used rhodamine dye dissolved in saline milk solutions. Altering the salinity varies the solution density, and thus flow at multiple depths can be observed; milk acts to stabilize the solution and slow diffusive dissipation.

Median grain size for the streambed is greater in the mid-channel [mean of the median grain size (\bar{X}) for all eight dam sites = 857 μ m, SEM = 50 μ m], and in coarse patches (\bar{X} = 2000 μ m, SEM = 600 μ m) than in the fine sediments (\bar{X} = 179 μ m, SEM =

Table 1 Size, architecture and channel position of study debris dams. Size is based on surface area of the streambed covered by wood; architecture is described by the length and diameter of the main log (dam “backbones” are from single treefalls), the angle of the log with the bank, and the angle of the main log with the plane formed by the streambed (i.e. the steeper the angle, the more the log protrudes up into the flow). Channel position indicates the distance from the nearest bank of the most upstream part of the dam and of the most downstream part

Parameter	Dam number							
	1	2	3	4	5	6	7	8
Area covered by dam on streambed (m ²)	3.8	23.4	14.8	33.6	9.2	21.8	32.5	8.6
Total number of logs ^a	1	2	1	3	2	1	2	2
Length of main log (m)	4.3	14.3	13.0	6.4	5.6	4.3	31.5	9.5
Diameter of main log (m) ^b	0.5	1.0	0.3	0.4	0.3	0.5	1.2	0.3
Number of branches off main log (s) ^c	2	5	6	5	2	8	6	4
Angle of main log from bank (°)	7	20	10	10	20	30	65	0
Angle of main log from sediment surface (°)	16	0	4	5	5	35	30	0
Channel position upstream (m) ^d	3	5	1	1	0	0	0	3
Channel position downstream (m) ^e	2.5	0	3.5	0	2.0	2.0	9.0	2.5

^a Logs were defined as pieces of wood longer than 1 m and larger than 0.1 m in diameter

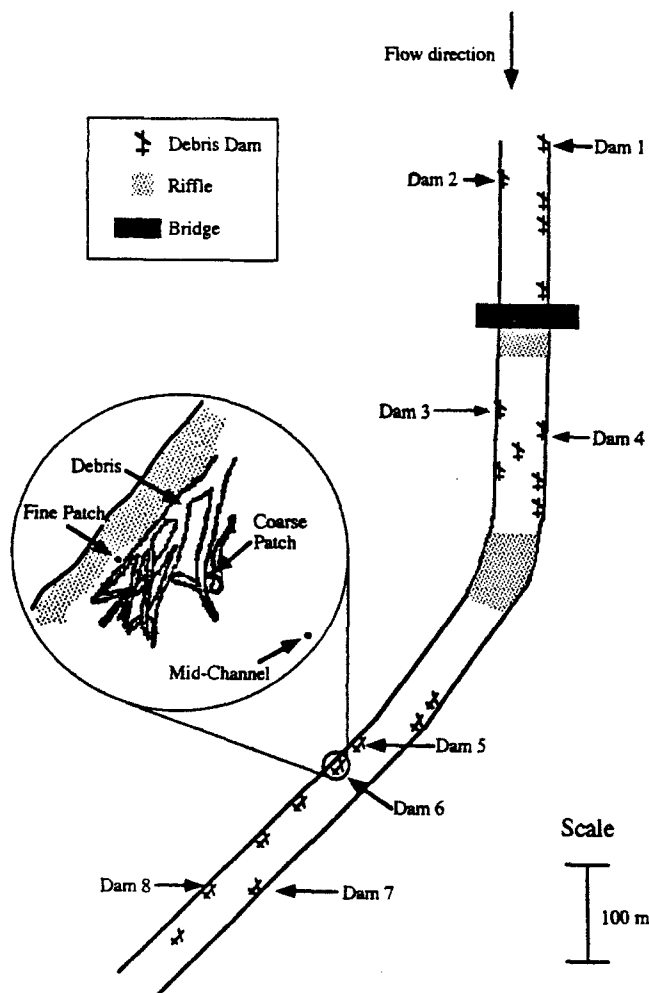
^b Main log was the largest log in a dam; most of a dam's complexity came from this single log

^c Branches were at least 0.5 m in length, 0.1 m in diameter

^d Distance from the most upstream part of the dam to the nearest bank

^e Distance from the most downstream part of the dam to the nearest bank

Fig. 1 A schematic of the study site, showing location of dam sites along the stream. Dams were numbered sequentially from upstream to downstream. Only large dams (i.e. dams produced by treefalls) are shown in this schematic; smaller woody debris is scattered along the entire streambed. Note – stream width exaggerated to show location of dams



13 μ m). The critical threshold for erosion of mid-channel substrate is ≈ 17 cm/s; for the poorly sorted, coarse substrate ≈ 17 –50 cm/s (different size particles moved at different flows); and for the fine sediments ≈ 28 cm/s (Palmer 1992; Palmer et al. 1995).

General sampling protocol and debris removal

To test hypothesis 1, we collected samples in the four patch types associated with each debris dam prior to, during, and following two floods (Fig. 2). We define floods as discharge events in which flows exceed the levels necessary to erode animals and bottom sediments (≈ 12 cm/s for animals; Palmer 1992). Our “during” flood samples (i.e. when flow still exceeded erosion thresholds) were collected as soon after peak discharge as was safely possible. To test hypothesis 2, we removed all of the woody debris in stretches 1 and 3 (dam sites 1, 2, 5, and 6; Fig. 1) on May 18–20, then we collected samples prior to, during, and following flood 2.

Debris was removed by sawing and carrying the wood into the surrounding forest. Within a week, we could not visibly detect signs of our work (i.e. no depressions in the streambed or footprints were visible). Post-manipulation sampling began 17 days after debris removal, because past work has shown that even sediments disturbed down to 30 cm are recolonized in less than 2 weeks (Palmer et al. 1992). Faunal abundances prior to the June flood did not differ between the debris-removed and debris-intact sites and thus the debris removal process itself had minimal impact on the fauna (Fig. 8 below).

Physical variables

Characterizing the flow regime in hydrodynamically complex areas like debris dams is not simple because the assumptions needed for the use of idealized fluid dynamics formulae are rarely met. We characterized the flow field by: (1) measuring near-bed flow (mean velocity at 2 cm above the streambed; hereafter, *bedflow*), (2) measuring depth-averaged flow (depth-integrated mean velocity divided by total water depth; Gordon et al. 1992), and (3) calculating rates of fluid flux per unit area at each sampling point (integrating the area under the plotted curves of mean flow versus depth, as in Eckman 1987). These three flow parameters were determined on each sampling date in the fine, coarse, and mid-channel patches of each dam site by taking velocity measurements in 5-cm intervals from the water surface to 2 cm above the streambed. A Marsh-

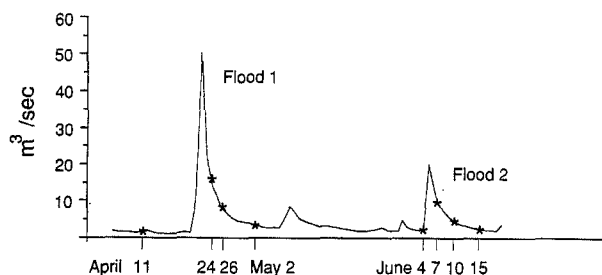


Fig. 2 Mean daily discharge of Goose Creek, Va. at the sampling area from April 1 through June 18, 1992 from the Virginia State Water Control Board; the gauge is located ≈ 50 m upstream of dam site 1. The critical threshold for sediment erosion in the mid-channel occurs at a discharge of approximately $6.5 \text{ m}^3/\text{s}$. Asterisks indicate sampling dates

McBirney electromagnetic meter (Model 201) was used which averages current velocity over a vertical distance of < 2 cm and is accurate to ± 0.6 cm/s. We could not measure velocity in the debris itself. A flow probe with a higher spatial resolution (e.g. hot-bead thermistor) would be required for measuring flow between leaves, and such probes are too delicate for field use during floods.

We collected a sediment sample from the fine, coarse, and mid-channel patches of each dam on each sampling date to determine median grain size, sorting, and percentage silt content (Buchanan 1984). We also surveyed along cross-sectional transects encompassing each dam to record the surface area of streambed that consisted of coarse substrate (gravel and small rocks mixed with sand), fine substrate (silts and clays), or well-sorted sands.

Faunal sampling

On each sampling date, we collected three replicate faunal samples from each patch type around each dam. Thus, for flood 1, we sampled in the coarse, fine, debris, and mid-channel patch types for all eight dams; in flood 2, we sampled these four patch types for the four intact dams. Since dams 1, 2, 5, and 6 were removed prior to the second flood, we collected our flood 2 samples for these four "sites" at three points along a cross-stream transect located where the dam was prior to removal. The sampling points along each transect were chosen to include a mid-channel position, a coarse sediment area, and a fine sediment area. Since the latter two patches were not associated with dams, they were not directly comparable to the fine and coarse patch types associated with dams. To emphasize this distinction, we refer to these sampling patches in the debris-removed stretches as *coarse (transect)* and *fine (transect) patches*.

Animals present in the debris of each dam were sampled by collecting three replicate "handfuls" of debris. Animals were rinsed from the debris onto $44\text{-}\mu\text{m}$ sieves and preserved in formalin. From the debris, twigs were hand measured (diameter and length) and surface area calculated assuming they were cylinders. Leaf surface areas were measured with an image analysis system. We then calculated the number of fauna per unit surface area of leaves/twigs. Each time we sampled, we estimated the fraction of the streambed underneath a dam that was covered with debris and the percentage of debris in a dam that we sampled; thus we report faunal abundances in the debris per m^2 of the streambed.

Animals present in the sediment patches were sampled by coring (2.5 cm diameter) to a depth of 10 cm. Prior work has shown that animals in Goose Creek do not migrate down into the hyporheic zone in response to floods and that faunal losses and recovery during floods are tractable by examining top sediment layers (Palmer et al. 1992). The sediment cores were placed in a solution of 1% MgCl_2 for ≈ 3 min to promote faunal relaxation, rinsed through a $44\text{-}\mu\text{m}$ mesh sieve, and preserved. In the laboratory, animals were

extracted via elutriation (Palmer and Strayer 1995) and then identified to major taxa.

Statistical analyses

Hypothesis 1: effect of floods on fauna in patches near dams versus open channel

Throughout, parametric statistical tests were performed on log $(x + 1)$ transformed abundances after determining that assumptions for the tests were met. Our analyses for testing hypothesis 1 involved three steps. First, a multivariate repeated measures analysis of variance (ANOVA) was performed to determine if abundances over time in each patch type were a function of stretch and dam site (dam nested within stretch). Because we found significant ($P < 0.001$) dam and stretch effects (i.e. dams within a stretch were no more similar than dams between stretches) and we wanted to look closely at the faunal response to floods on a dam-by-dam basis, we chose to conduct separate two-way ANOVAs for each dam site (eight dams in flood 1, four in flood 2) to determine if the number of fauna depended on both date and patch type (four dates \times four patch types with three replicate samples for each). The critical statistic for this step in our analysis was the date \times patch interaction term since it would indicate if changes in faunal abundance over time in each dam varied among patch types.

Secondly, we made post hoc comparisons of mean faunal abundance pre-flood versus flood for each patch within each dam using the REGW F -test with the maximum experiment-wise error rate specified as 0.05 (SAS 1989). We focused on the pre-flood versus flood dates for these comparisons to determine if the immediate impact of flooding on faunal abundances (i.e. immediate response to the onset of high flow) differed among patch types. Thus, our specific comparisons for flood 1 were April 11 (pre-flood) versus April 24 (flood) and for flood 2 were June 4 versus June 7.

Our third step in the analysis for testing hypothesis 1 was to use the results of the post hoc comparisons to ask if there was statistical evidence in general (i.e. when results from all the dams were considered) that the faunal response to floods varied among patch types. "Response" refers to a decrease, increase, or no change in faunal abundance at flood onset. We categorized our data in this fashion (i.e. according to the direction of faunal response) because an increase or no change in faunal abundances in a patch during a flood would suggest that the patch is acting as a refuge. We used a Kruskal-Wallis test to test the null hypothesis that there was no difference in the distribution of responses among patches, e.g. the number of dams that showed significant increases in faunal abundances during a flood did not vary among patch types. This non-parametric rank statistic tests for an association between the row variable (patch type) and the ordinal column variable (faunal response). To perform the Kruskal-Wallis test we invoked the Cochran-Mantel-Haenszel option in SAS's Proc Freq (SAS 1989). Here, the Kruskal-Wallis test is a meta-analysis since we pool the statistical findings of several identically conducted experiments. Although for each dam we conducted a separate analysis (ANOVA) with its own type-I error, the pooling provides a statistical criterion for assessing the overall pattern (i.e. over all dams). We performed separate Kruskal-Wallis tests for floods 1 and 2 and for each taxon to ensure independence of data.

Hypothesis 2: effect of debris removal

A repeated measures ANOVA was performed to determine if the abundance of fauna in the mid-channel was a function date and treatment (debris removed versus debris intact) interaction. The effect of interest in testing our hypothesis was the date \times treatment interaction. A significant interaction would indicate that the effect

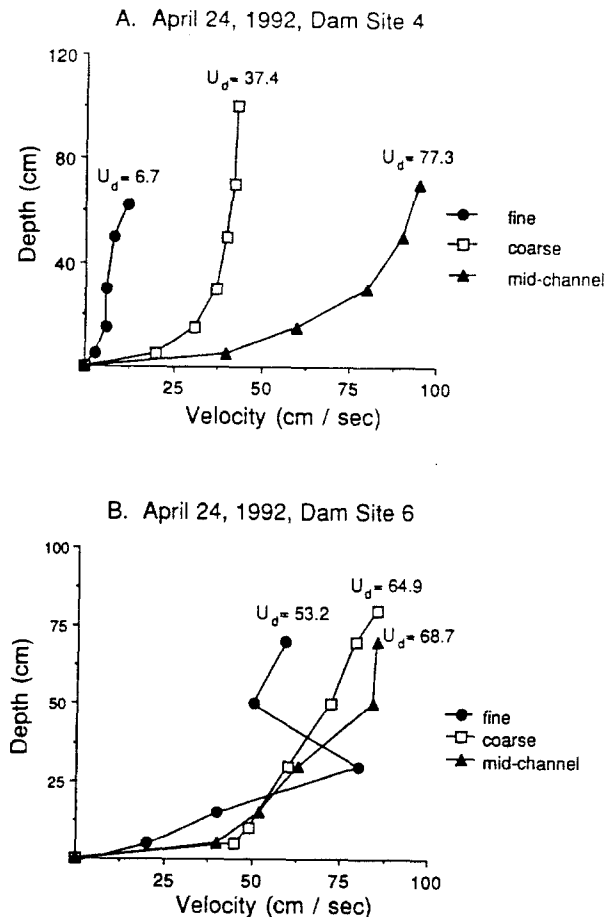
of the flood on faunal abundances depended on whether or not debris had been removed. We focused on the response of fauna in the mid-channel because this site was directly comparable between debris-removed and debris-intact sites and it contained the most common patch type for the stream. We also used ANOVAs to: (1) examine faunal responses in the other debris-removed patch types [coarse (transect) and fine (transect) patches] to determine if abundances changed during the flood; and (2) determine if the proportion (arcsin transformed) of silts and clays in the debris-intact and debris-removed sites changed from the pre-debris removal dates (April 11) to the post-removal (June 4) survey dates.

Results

Physical variables

The magnitude of flood 1 (peak velocity mid-channel ≈ 75 cm/s) was greater than that of flood 2 (≈ 50 cm/s) and discharge returned to approximately pre-flood levels sooner for flood 2 (Fig. 2). In both cases, scouring was visible in the mid-channel and the critical erosion velocity for the animals was exceeded. In Goose Creek, the water level rarely exceeds bank-

Fig. 3A, B Vertical velocity profiles at the fine, coarse, and mid-channel patches for two dam sites (A, B) (other sites displayed comparable velocity profiles) during flood 1. Depth is distance above the streambed. U_d depth averaged velocity in cm/s (see Materials and methods for explanation)



Flood 1: Chironomids

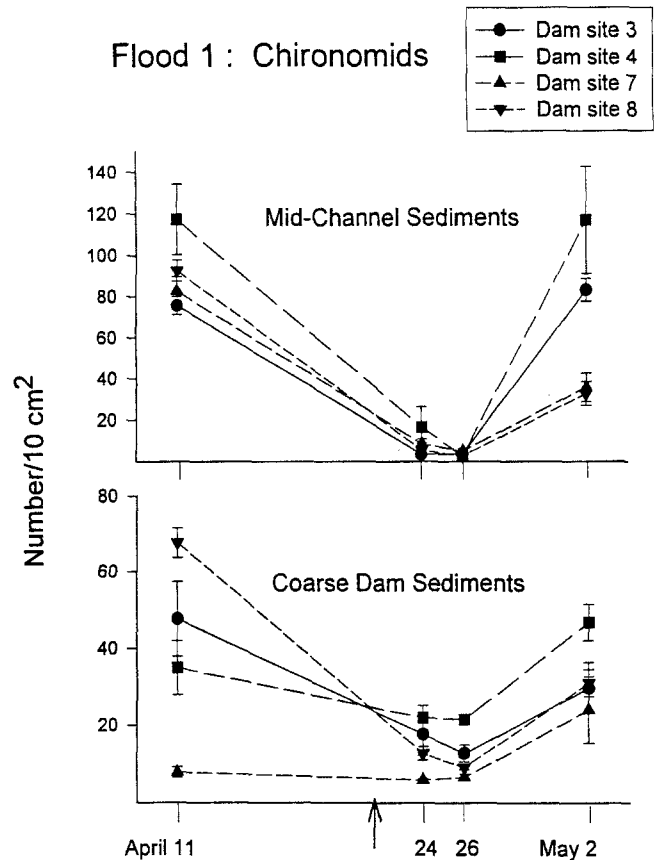


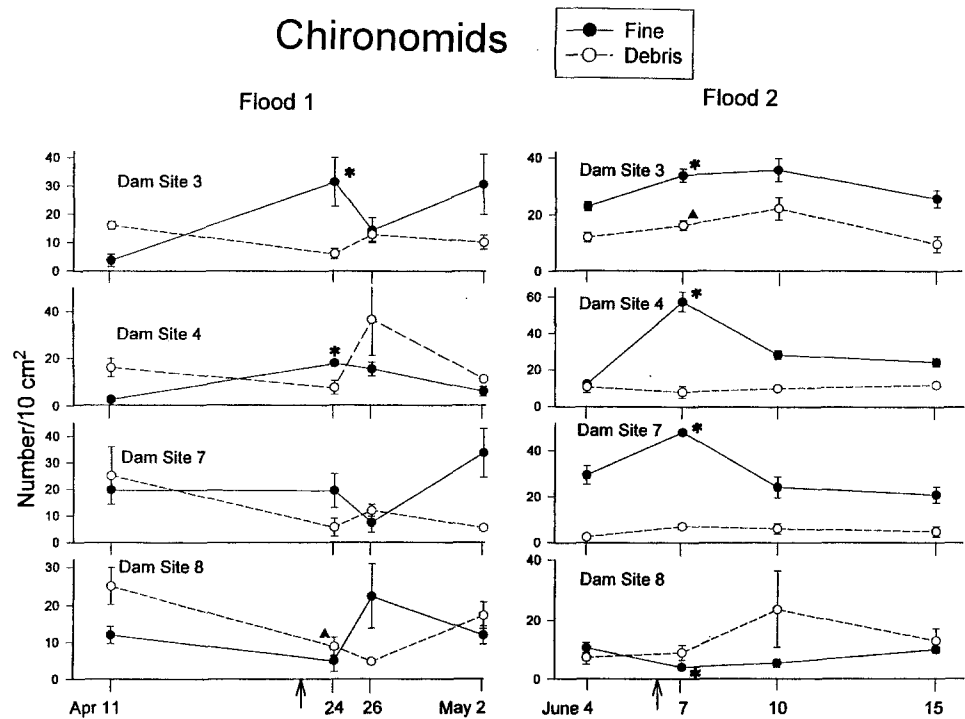
Fig. 4 Mean abundance (± 1 SEM) of chironomids prior to, during, and following flood 1 in the coarse and mid-channel patches associated with four of the dam sites. General pattern of reduced abundances following the flood with no or partial increases in abundances by last sampling date was found for all taxa and for dam sites not shown. Arrow indicates onset of flood. Here and in all figures, error bars are obscured by data point symbols in some places

full and did not do so during these floods. The dams were not moved by either flood. For all dam sites and both floods, current velocity and water flux were significantly higher in mid-channel and coarse patches than in fine sediment patches, although the magnitude of the flow differences among patches varied between dam sites (Fig. 3).

Test of hypothesis 1: effect of floods on fauna in patches near dams versus open channel

The impact of floods on invertebrate abundances varied among patches and, for some patch types, among dams. For all taxa, dam sites and floods, there was a significant date \times patch interaction effect (ANOVA, $P < 0.001$ in each case) on faunal abundance. To illustrate faunal response, data from both floods are presented graphically (Figs. 4–6) for dam sites that were present for the duration of the study (sites 3, 4, 7, 8). Data for dams that were removed after flood 1 (sites 1, 2, 5, 6) are provided in Table 2.

Fig. 5 Mean abundance (± 1 SEM) of chironomids prior to, during, and following each flood in the fine sediment patches and debris associated with dams 3, 4, 7, and 8 (see Table 2 for sites 1, 2, 5, and 6). *Asterisks* (fine patches) and *triangles* (debris) above data points indicate statistically significant changes in abundance near peak flooding compared to pre-flood ($P = 0.05$, REGW-F post hoc comparisons tests). *Arrows* indicate flood onset



The faunal response to flooding differed among dams for only some patch types. In the mid-channel and coarse patches, post hoc comparisons showed that abundances of both chironomids and copepods decreased markedly during both floods, with no or partial increases in abundance by the last sampling date. For brevity, Fig. 4 shows flood 1 data for chironomids only, although similar patterns were found for all taxa and dams. In the fine and debris patches, chironomid and copepod abundances decreased, increased or did not change significantly depending on dam site and flood (Figs. 5, 6; Table 2). A summary of the number

of dams exhibiting various faunal responses further illustrates that the immediate impact of increased flow was dam and flood specific (Table 3).

The "global" test for an effect when considering all dams (Kruskal-Wallis test, Table 3), showed that the faunal response did vary significantly among patches. Chironomid abundances in debris and fine patches were less likely to decline during a flood than in the mid-channel or coarse patches for flood 1 ($P = 0.006$) and for flood 2 ($P = 0.028$). Similarly, copepod abundances in the fine or debris patches were less likely to decline during flood 2 than in the mid-channel or coarse

Table 2 Mean number (SEM) of copepods and larval chironomids before (April 11), during (April 24, 26) and after (May 2) flood 1. Data are shown for the fine sediment and debris patches associated with dam sites 1, 2, 5, and 6; see Figs. 5–6 for dams 3, 4, 7, and 8.

Asterisks indicate significant changes in abundance near peak flooding (April 24) compared to pre-flood (April 11) ($P = 0.05$; REGW-F post hoc comparisons described in text)

Site	Abundance of:							
	Copepods				Chironomids			
	April 11	24	26	May 2	April 11	24	26	May 2
Fine patch dam site								
1	9.7 (1.7)	0*	4.7 (2.3)	0	45.0 (8.7)	7.7 (0.9)*	26.7 (6.4)	12.7 (1.7)
2	6.7 (0.7)	7.7 (2.0)	5.3 (1.3)	0.7 (0.7)	18.7 (2.8)	13.0 (2.0)	13.7 (3.5)	16.3 (6.2)
5	2.0 (1.2)	0.3 (0.5)	0	0	14.0 (1.2)	40.3 (5.6)*	2.7 (2.7)	5.3 (1.5)
6	13.3 (1.3)	0*	0	0	5.3 (1.3)	5.1 (1.3)	11.0 (1.5)	23.7 (8.2)
Debris patch dam site								
1	0.1 (0.06)	0.10 (0.03)	0.02 (0.02)	0.30 (0.07)	4.1 (1.4)	2.3 (1.4)	0.8 (0.2)	1.3 (0.4)
2	0.6 (0.2)	0.04 (0.04)	0	0.03 (0.01)	3.0 (0.3)	0.2 (0.06)*	0.5 (0.2)	0.7 (0.3)
5	0.6 (0.2)	0.02 (0.01)	0.20 (0.1)	0.08 (0.03)	2.4 (1.0)	1.2 (0.5)	3.5 (1.1)	0.7 (0.2)
6	0.8 (0.5)	0.01 (0.01)*	0.04 (0.04)	0.07 (0.06)	5.5 (0.8)	0.3 (0.2)*	1.2 (0.2)	0.9 (0.1)

Table 3 A summary of the number of dams exhibiting different faunal responses (↓, decreased abundance; ↑, increased abundance; NC, no change) by patch type [mid-channel (MC), coarse, fine, or debris] and for each flood, e.g. for flood 1, there was a statistically significant decrease in the abundance of copepods in the mid-channel at 7 of 8 dam sites. Responses are based on the results of the post hoc comparisons tests provided in Figs. 5, 6 and Table 2

Patch type	Faunal responses					
	Chironomids					
	Flood 1 ^a			Flood 2 ^b		
	↓	NC	↑	↓	NC	↑
MC	8	0	0	4	0	0
Coarse	6	2	0	3	1	0
Fine	1	4	3	1	0	3
Debris	3	5	0	0	3	1

Patch type	Copepods					
	Flood 1 ^c			Flood 2 ^d		
	↓	NC	↑	↓	NC	↑
	↓	NC	↑	↓	NC	↑
MC	7	1	0	4	0	0
Coarse	4	4	0	3	1	0
Fine	4	3	1	2	2	0
Debris	4	4	0	0	2	2

^a $P = 0.006$, ^b $P = 0.028$, ^c $P = 0.325$, ^d $P = 0.037$. Results of the Kruskal-Wallis test (for each flood and each taxon) of the null hypothesis: no difference in the distribution of faunal responses (↓, ↑, or NC) among patches. $N = 8$ dams during flood 1 and 4 dams (unmanipulated sites) during flood 2

patches ($P = 0.037$). During flood 1, however, a high incidence of the “no change response” occurred not only in the fine and debris patches, but also in the coarse

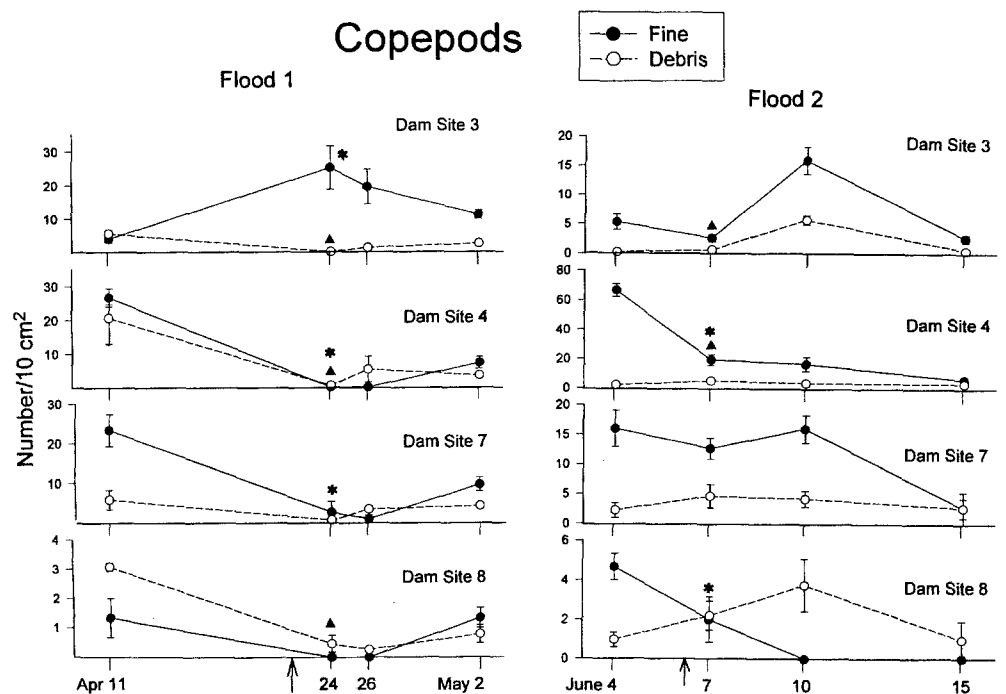
sediments near dams and, thus, the distribution of faunal responses was not significantly different across the four patches during this flood ($P = 0.325$; Table 3).

Linking physical processes to the accumulation of animals in patches

We examined a variety of dam-specific characteristics to ask if there were unique features of some dams that may explain why faunal abundances (mostly chironomids) increased during floods in the fine or debris patches of some dams (dams 3–5 in flood 1 and dams 3, 4, and 7 in flood 2) but decreased in other dams. We examined five physical variables that were most likely related to the retention and/or settlement of fauna around dams during floods. These included whole dam attributes (size of dam, angle of dam to streambed, distance from stream bank) and patch-specific flow measurements (bedflow, flux) made during the floods. We used flow data from the fine sediment patches since velocity could not be measured among the leaves and twigs of debris patches.

We used discriminant analysis (SAS 1989) to ask if we could statistically separate the dams that accumulated animals from dams that did not, based on the five physical variables. The analysis was able to successfully distinguish ($P = 0.004$) the two groups of dams solely in terms of the physical variables. Three variables were particularly important in separating the two groups of dams; univariate F -tests indicated that near-bed flow ($P = 0.0018$) and water flux ($P = 0.0042$) were highly significant, while the distance of a dam from the bank ($P = 0.0724$) had somewhat less

Fig. 6 Mean abundance (± 1 SEM) of copepods prior to, during and following floods in the fine sediment patches and debris associated with dams 3, 4, 7, and 8 (see Table 2 for sites 1, 2, 5, and 6). Asterisks (fine patches) and triangles (debris) above data points indicate statistically significant changes in abundance near peak flooding compared to pre-flood ($P = 0.05$, REGW-F post hoc comparisons). Arrows indicate flood onset



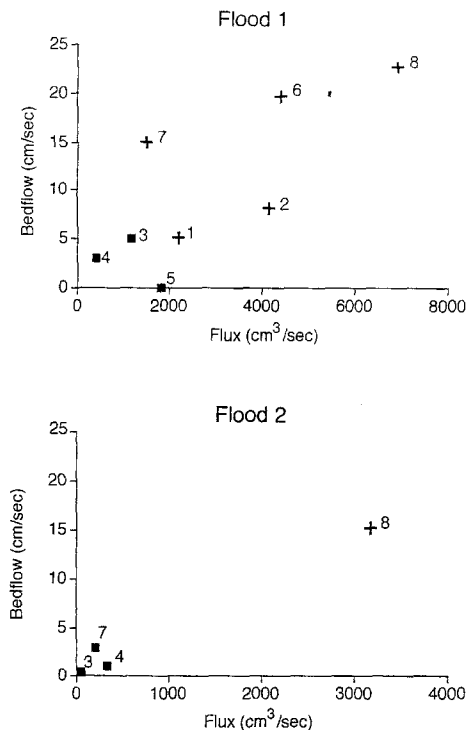


Fig. 7 Near-bed velocity and water flux measured during floods 1 and 2 for the fine sediment patches that accumulated animals during the flood (*square symbols*) and for the remaining fine sediment patches (*cross symbols*); see text for full explanation. The dam site number is indicated next to each symbol

discriminatory power. In general, only fine sediment patches in dams with low bedflow and low water flux accumulated animals during a flood (Fig. 7).

Test of hypothesis 2: effects of debris removal

In general, debris removal did not impede faunal recovery in the mid-channel. There was no significant treatment \times date effect for total meiofauna ($P = 0.168$; Fig. 8) or for chironomids alone ($P = 0.198$). For copepods, there was a significant interaction ($P = 0.041$), but it was due to an increase in abundances in a single dam on one date. In all dam sites, faunal abundances mid-channel decreased at the flood onset and then increased to varying extents post-flood (Fig. 8). We found no evidence of higher abundances during the flood at any other sampling points in the debris-removed sites [i.e. fine or coarse (transect) sites] that might offset losses in the mid-channel (Fig. 9).

Removal of debris was associated with a decrease (marginally significant at $P = 0.059$) in the amount of silt and clay sediments. Prior to removal of the woody debris (on April 11), the mean percentage of cross-sectional area covered by fine sediments in debris-intact sites ($N = 4$) was 21.6% (SEM = 4.8%) and for the sites that would later have debris removed ($N = 4$) it was 18.7% (SEM = 4.3%). Then, 2 weeks after debris

removal (on June 4), this was 18.5% (SEM = 3.6%) in debris-intact sites and 8.9% (SEM = 3.3%) in sites with no debris.

Discussion

A variety of studies have suggested that in frequently disturbed environments, movement of animals among different habitat patches may promote persistence (May and Southwood 1990; Pulliam 1988; Turner 1987), particularly if there is substantial spatial variation in disturbance effects (Lefkovich and Fahrig 1985; Pickett and White 1985). In this paper, we show that the effect of a disturbance varied markedly among patch types in a low-gradient, warmwater stream. In the dominant patch type, the sandy mid-channel, and in the coarse sediment patches near debris dams, large numbers of animals (40–95%) were lost from the streambed during floods. These patch types are the most unstable of those studied because: (1) they have the lowest thresholds for initiation of substrate movement; (2) these thresholds are higher than those necessary to erode the fauna; and (3) flow in these patches during floods exceeded both the sediment and faunal erosion thresholds. Additionally, grain size varied more in the mid-channel and coarse patch types during a flood (i.e. between sampling dates) than in fine sediment patches (Palmer et al. 1995). In the fine patches, flows were below critical erosion velocities for the fine sediments during our flood sampling. Not only did these patches retain fine sediments throughout the floods, but in some dams they retained or concentrated animals. The patches accumulating animals were those with low near-bed velocity and water flux, even during floods. The remarkable match between biotic pattern (accumulation of animals) and underlying physical processes (reduced flow plus stable substrate) was found for both of the floods we studied.

Overall dam attributes (e.g. dam size) were not generally useful in predicting which dams harbored patches that accumulated animals. We had expected large dams (site 8) or dams with many branching pieces (site 6) to reduce flow and enhance faunal settlement during floods. This was not the case, presumably because flow is so complex in and around debris dams. The fact that the fine patch in dam 7 accumulated animals during flood 2 but not during flood 1 further demonstrates that whole dams simply cannot be labeled as refugia per se. Although structural complexity is assumed to be important in generating biotic pattern in many ecosystems (Bell et al. 1991), our work underscores the need to understand what processes are responsible for the link between physical structure and biotic pattern.

Refugia have been defined explicitly by stream ecologists as patches which confer spatial and temporal resistance or resilience to biotic communities (Fisher 1990; Sedell et al. 1990). Resistance may result in

Flood 2: Mid Channel

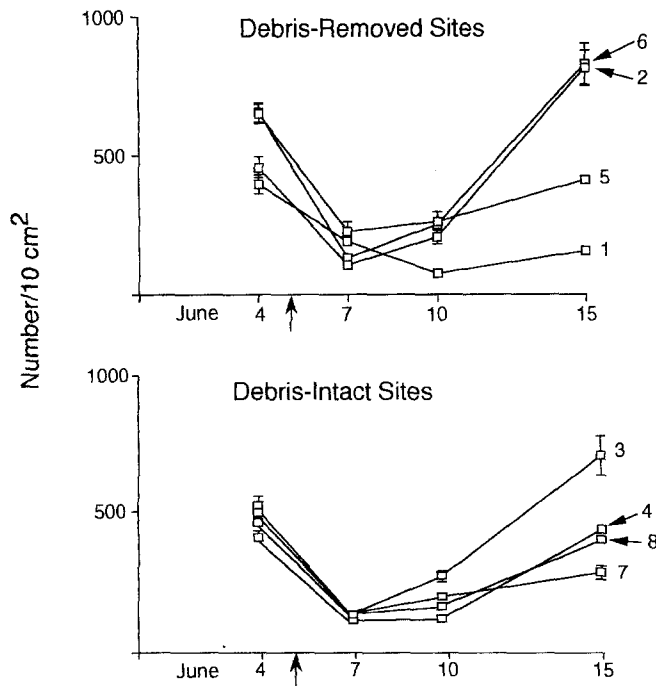
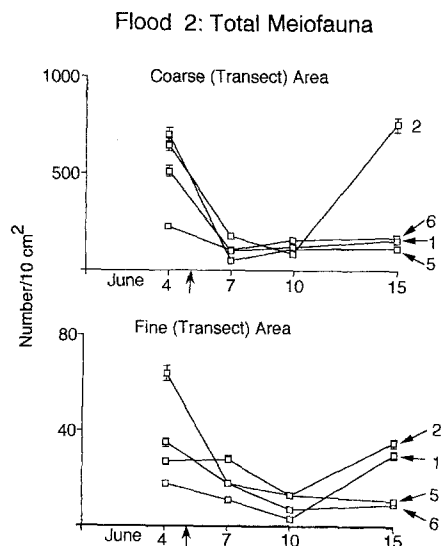


Fig. 8 Mean abundance (± 1 SEM) of total meiofauna (copepods, chironomids, nematodes, rotifers, oligochaetes) during flood 2 in mid-channel patches that were not manipulated (debris-intact) and in patches from which all of the woody debris had been removed prior to the flood (debris-removed). Total meiofauna are shown since all fauna displayed similar patterns. Dam site number is indicated next to each line. Arrows indicate onset of flood

Fig. 9 Mean abundance (± 1 SEM) of total meiofauna prior to and following flood 2 at the coarse and fine sediment sampling areas in the transects associated with debris-removed sites. Note – since all debris was removed from these sites, the coarse and fine (transect) sampling areas cannot be directly compared to the coarse and fine patches at sites with intact dams



little or no change in faunal abundance in response to disturbance, and resilience in a rapid return to pre-disturbance levels (Harrison 1979). For streams, flow refugia have been defined as patches that experience relatively low hydraulic stress during spates; they may enhance faunal resistance or resilience (Lancaster and Hildrew 1993). Animals need not move *actively* into a patch for it to serve as a flow refugium; fauna may be passively relocated into the patch or may remain in the patch during spates (Robertson et al. 1995). The important point is that animals accumulate and/or survive differentially in refuge patches (Hildrew and Giller 1994; Robertson et al. 1995). Often this is assumed to be directly related to substrate stability (e.g. see Death and Winterbourn 1994 and references within). In our study, since all fine patches retained sediments during floods, substrate stability was not the defining characteristic of refugia; low flow/water flux plus substrate stability defined refugia.

Our finding of no change, or even increases, in faunal abundances at the peak of flooding in some debris and fine sediment patches suggests that both patch types have the potential to act as flow refugia. Golladay and Hax (1995) provided evidence that chironomids and copepods may cling to debris during floods whether it is floating or intact. In our study, we found low and highly variable faunal abundances in the debris; therefore, we do not believe the evidence is strong enough at this time to label the leaves and wood as flow refugia. The evidence that some fine sediment patches acted as flow refugia in Goose Creek is stronger. First, the meta-analysis indicated that increased faunal abundances at the peak of flooding in the fine sediments of some dams was not due to chance alone. Secondly, and perhaps more importantly, we could distinguish fine sediment patches that accumulated animals from those that did not, based solely on their physical attributes (discussed more fully below).

The term refugia implies reduced mortality; unfortunately direct measurement of mortality during floods is difficult, if not impossible, for most stream benthos, since the fate of individuals is not tractable. Stream ecologists studying disturbance have used the term *mortality* almost interchangeably with *low resistance* when faunal abundances decline in response to floods (e.g. Fisher and Grimm 1991; Scarsbrook and Townsend 1993). However, changes in faunal abundance due to flooding may result from mortality or from the flux of individuals among patches or between the streambed and the drift. Indeed, the enhanced abundances we observed in some fine sediment patches may have been due to deposition of individuals from the drift (Palmer 1992). This does not negate a refuge effect since, for both meiofauna and macrofauna, time spent in the water column may have negative consequences including enhanced mortality from starvation and predation (Allan 1995; Palmer 1988, 1992; Thistle et al. 1995). If

patches within debris dams enhance deposition, thereby shortening the time animals spend in transport, then the patches may reduce mortality.

There is some support for the deposition interpretation since fine patches accumulated animals during a flood if flow near the sediment-water interface was low and water flux through the site was low. If either was "high", then animals did not accumulate in patches. For example, during flood 1, even though near-bed flow in the fine patch of dam 1 was only 5 cm/s, animals did not accumulate here, presumably because flux was too high (Fig. 7). The high flux values were due to a flow acceleration at mid-depth in the fine patch (probably caused nearby wood). In dam site 3, bedflow was comparable to that in dam 1, but flux was lower and animals accumulated in the fine sediments (Fig. 7).

Since flux is the rate of fluid transport above a site (i.e. the depth integral of velocity), it can indicate complex flow patterns in the water column above, such as mid-depth flow accelerations (e.g. Fig. 3B, profile for fine site). Indeed, it has been used to characterize the effects of physical structures on flow in other benthic studies (e.g. Eckman 1983, 1987). These effects may include the creation of eddies intermittently impinging on the bottom causing high shear stresses and erosion locally. These eddies may prevent faunal settlement or retention on the bottom (Eckman 1987, 1990). Since one may obtain similar flux values for different reasons, it is useful to examine the velocity profiles when interpreting flux values.

Interestingly, flux should also be related to the supply of copepods and chironomids drifting past a point, since, for these animals, the probability of entering the drift increases as flow increases (Palmer 1992). The fact that high flux values were not associated with faunal accumulation at a site suggests that the processes of settlement (deposition) and retention on the bottom due to low bottom shear are more important in determining faunal abundance during a flood than is the supply of drifting animals.

Although we were unable to obtain estimates of shear stress from our velocity profiles (see Materials and methods), near-bed velocity provides a reasonable approximation of near-bed forces (Gordon et al. 1992). The bedflow values suggest that the fine sediment patches that accumulated animals were depositional. Species level information also supports deposition as the process whereby faunal abundances were enhanced in some patches. Copepod and chironomid species composition in the "refugium" patches (those accumulating animals) changed more in response to the floods than in the nonrefugium patches, due to an influx of individuals from just a few species (Palmer et al. 1995).

Despite evidence that deposition was enhanced in specific patches associated with debris dams, recovery of animals was no lower in debris-removed sites than in those with intact dams. This was somewhat surpris-

ing since shear stress and bedload transport typically increase following removal of woody debris (Smith et al. 1993) and we found that the debris-removed dam sites were indeed dominated by coarser substrates than were sites with intact debris dams. Because copepods and larval chironomids are passively eroded and deposited, we expected the floods to have greater impacts in debris-removed stretches. Since recovery had begun in these stretches by our last sampling date following flood 2, such patches were apparently not essential to faunal recovery stream-wide in Goose Creek. Indeed, the high faunal abundances in mid-channel sediments and the dominance of this patch type stream-wide in comparison to the relatively low faunal abundances in the fine patches further indicate that the latter patches can not explain recovery stream-wide.

Perhaps there are yet other refugia we have not studied that contribute to the resilience of these fauna, particularly in the mid-channel. Our present study and past work (Palmer et al. 1992) make it clear that post-flood recovery in Goose Creek is likely due to a combination of processes including the utilization of refugia (potentially including debris dams), survival in the drift with resettlement to the bottom, and reproduction. Differentiating among these processes and assessing their relative importance are nontrivial problems.

Acknowledgements We wish to thank the following people for providing assistance in the field or laboratory: A. Bahr, R. Boerner, C. Carlson, E. Daly, J. Higgins, M. Jankowski, E. Janus, P. Lorch, T. Manuelides, M. Nussman, N. L. Poff, M. Saunders, and especially C. Hakenkamp. P. Botts and J. Reid provided invaluable taxonomic expertise. P. Botts, A. Boulton, D. Breitburg, C. Hakenkamp, J. Lancaster, N. L. Poff, M. Shofner, D. Smith, B. Turner and anonymous reviewers made constructive comments on the manuscript. This work was supported by grants to M. Palmer from the National Science Foundation (BSR9006002, DEB 9106781) and the Maryland Agricultural Experiment Station.

References

- Allan JD (1995) Stream ecology: structure and function of running waters. Chapman and Hall, New York
- Bell SS, McCoy ED, Mushinsky HR (1991) Habitat structure: the physical arrangement of objects in space. Chapman and Hall, New York
- Berger ML (1994) Diel variation in drift distance of freshwater benthic invertebrates in Goose Creek, Va. Honors Thesis, University of Maryland, College Park, Md., USA
- Bilby RE (1981) Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* 62: 1234-1243
- Borchardt D (1993) Effects of flow and refugia on drift loss of benthic macroinvertebrates: implications for habitat restoration in lowland streams. *Freshwater Biol* 29: 221-227
- Boulton AJ, Peterson CG, Grimm NB, Fisher SG (1992) Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73: 2192-2207
- Bretschko G (1990) The dynamic aspect of coarse particulate organic matter on the sediment surface of a second order stream free of debris dams (RITRODAT-LUNZ study area). *Hydrobiologia* 203: 15-28

- Buchanan JB (1984) Sediment analyses. In: Holme NA, McIntyre AD (eds) *Methods for the study of marine benthos*. Blackwell Scientific Publishers, Oxford, pp 41–65
- DeAngelis DL, Waterhouse JC (1987) Equilibrium and non-equilibrium concepts in ecological models. *Ecol Monogr* 57: 1–21
- Death RC, Winterbourn MJ (1994) Environmental stability and community persistence: a multivariate perspective. *J North Am Benthol Soc* 13: 125–139
- Eckman JE (1983) Hydrodynamic processes affecting benthic recruitment. *Limnol Oceanogr* 28: 241–257
- Eckman JE (1987) The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* within eelgrass meadows. *J Exp Mar Biol Ecol* 106: 165–181
- Eckman JE (1990) A model of passive settlement by planktonic larvae onto bottoms of differing roughness. *Limnol Oceanogr* 35: 887–901
- Fisher SG (1990) Recovery processes in lotic ecosystems: limits of successional theory. *Environ Manage* 14: 725–736
- Fisher SG, Grimm NB (1991) Streams and disturbance: are cross-ecosystem comparisons useful? In: Cole J, Lovett G, Findlay S (eds) *Comparative analyses of ecosystems*. Springer, Berlin Heidelberg New York, pp 196–222
- Golladay SW, Hax CL (1995) Effects of a man-made flow-disturbance on meiofauna in a north Texas prairie stream. *J North Am Benthol Soc* 14: 404–413
- Gordon ND, McMahon TA, Finlayson BL (1992) *Stream hydrology: an introduction for ecologists*. Wiley, Chichester
- Harrison GW (1979) Stability under environmental stress: resistance, resilience, persistence, and variability. *Am Nat* 120: 659–669
- Hildrew AG, Dobson MK, Groom A, Ibbotson A, Lancaster J, Rundle SD (1991) Flow and retention in the ecology of stream invertebrates. *Verh Int Ver Theor Angew Limnol* 24: 1742–1747
- Hildrew AG, Giller PS (1994) Patchiness, species interactions and disturbance in the stream benthos. In: Giller PS, Hildrew AG, Raffaelli DG (eds) *Aquatic ecology: scale, pattern and process*. 1992 Symposium at University College, Cork, UK. Blackwell Scientific Publications, Oxford. 34th Symposium of the British Ecological Society, pp 21–62
- Lancaster J, Hildrew AJ (1993) Flow refugia and the microdistribution of lotic macroinvertebrates. *J North Am Benth Soc* 12: 385–393
- Lefkovich LP, Fahrig L (1985) Spatial characteristics of habitat patches and population survival. *Ecol Modell* 30: 297–308
- Marmonier P, Crueze des Châtelliers M (1991) Effects of spates on interstitial assemblages of the Rhone River. Importance of spatial heterogeneity. *Hydrobiologia* 210: 243–251
- May RM, Southwood TRE (1990) Introduction. In: Shorrocks B, Swingland IR (eds) *Living in a patchy environment*. Oxford University Press, Oxford, pp 1–22
- Naiman RJ (1982) Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. *Can J Fish Aquat Sci* 39: 1699–1718
- Paine R (1966) Food web complexity and species diversity. *Am Nat* 100: 65–75
- Palmer MA (1988) Epibenthic predators and marine meiofauna: separating predation, disturbance, and hydrodynamic effects. *Ecology* 69: 1251–1259
- Palmer MA (1992) Incorporating lotic meiofauna into our understanding of faunal transport processes. *Limnol Oceanogr* 37: 329–341
- Palmer MA, Strayer DL (1995) Meiofauna. In: Hauer FR, Lamberti GA (eds) *Methods of stream ecology*. Academic (in press)
- Palmer MA, Bely AE, Berg KE (1992) Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia* 89: 182–194
- Palmer MA, Arensburger P, Botts PS, Hakenkamp CC, Reid J (1995) Disturbance and the community structure of stream invertebrates: patch-specific effects and the role of refugia. *Freshwater Biol* 34:
- Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics*. Academic, Orlando, Fla.
- Poff NL, Palmer MA, Angermeier PL, Vadas RL, Hakenkamp CC, Bely AE, Arensburger P, Martin AP (1993) Size structure of the metazoan community in a Piedmont stream. *Oecologia* 95: 202–209
- Pringle CM, Naiman R, Bretschko G, Karr JR, Oswood MW, Webster JR, Welcomme RL, Winterbourn ML (1988) Patch dynamics in lotic systems: the stream as a mosaic. *J North Am Benthol Soc* 7: 503–524
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132: 652–661
- Resh VH, Brown AV, Covich AP, Gurtz ME, Li HW, Minshall GW, Reice SR, Sheldon AL, Wallace JB, Wissman RC (1988) The role of disturbance in stream ecology. *J North Am Benthol Soc* 7: 433–455
- Robertson AL, Lancaster J, Hildrew AG (1995) Stream hydraulics and the distribution of microcrustacea: a role for refugia? *Freshwater Biol* 33: 469–484
- SAS Institute (1989) *SAS User's Guide*, version 6, 4th edn, vol 2. Cary, N.C.
- Scarsbrook MR, Townsend CR (1993) Stream community structure in relations to spatial and temporal variation: a habitat template study of two contrasting New Zealand streams. *Freshwater Biol* 29: 395–410
- Sedell JR, Reeves GH, Hauer FR, Stanford JA, Hawkins CP (1990) Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. *Environ Manage* 14: 711–724
- Smith RD, Sidle RC, Porter PE, Noel JR (1993) Effects of experimental removal of woody debris on the channel morphology of a forest, gravel-bed stream. *J Hydrol (Amst)* 152: 153–178
- Smock LA, Metzler GM, Gladden JE (1989) Role of debris dams in the structure and functioning of low-gradient headwater streams. *Ecology* 70: 764–775
- Sousa WP (1984) The role of disturbance in natural communities. *Annu Rev Ecol Sys* 15: 353–391
- Thistle D, Weatherly GL, Wonnacott A, Ertman SC (1995) Suspension by winter storms has an energetic cost for adult male benthic harpacticoid copepods. *Mar Ecol Prog Ser* (in press)
- Turner MG (ed) (1987) *Landscape heterogeneity and disturbance*. Springer, Berlin Heidelberg New York
- Wallace JB, Benke AC (1984) Quantification of wood habitat in subtropical coastal plains streams. *Can J Fish Aquat Sci* 41: 1642–1652
- Winkler G (1991) Debris dams and retention in a low order stream. *Verh Int Vereinig Theoret Angew Limnol* 24: 1742–1747