Ecology, 83(3), 2002, pp. 628–642

THE EFFECT OF HYDROLOGICAL DISTURBANCE ON THE IMPACT OF A BENTHIC INVERTEBRATE PREDATOR

JAMES R. THOMSON,[1,3] P. S. LAKE,[1] AND BARBARA J. DOWNES[2]

[1]*Department of Biological Sciences & Cooperative Research Centre for Freshwater Ecology, Monash University, Wellington Road, Clayton, Victoria 3168, Australia*
[2]*School of Anthropology, Geography and Environmental Studies, University of Melbourne, Melbourne, Victoria 3010, Australia*

Abstract. The harsh–benign model of community dynamics predicts that the impact of predation will decline as abiotic conditions become more stressful to biota. Experiments were conducted to determine whether hydrological disturbance altered the impact of an invertebrate predator in stream benthic communities. The impact of a predatory stonefly, *Cosmioperla kuna*, on its mayfly prey was measured in experimental stream channels receiving constant or variable flow (flooding) regimes over a one-week period. Contrary to predictions of the harsh–benign hypothesis, the impact of *Cosmioperla* on its two major prey taxa was either unchanged or increased by artificial floods, despite increased predator emigration from variable-flow channels. Predator impacts in variable-flow treatments were apparently strongly influenced by predator-induced prey emigration during floods. The results of this study show that nonlethal predator effects may be important during abiotic disturbance, and that it may not be reasonable to predict the impact of predation solely on the basis of the relative tolerances of predators and prey to prevailing abiotic conditions.

Key words: abiotic disturbance and lotic predator impacts; Cosmioperla kuna; *disturbance, stream benthic communities; environmental stress models; flood, impacts on lotic predators; harsh–benign model; predation; predator effects, indirect; stream benthic communities.*

INTRODUCTION

The interaction between biotic and abiotic processes in determining the composition, abundance and distribution of species within communities is a central concern of ecology (Connell 1975, Menge and Sutherland 1976, Hildrew and Giller 1994). The harsh–benign hypothesis (Connell 1975, Menge 1976, Menge and Sutherland 1976, Peckarsky 1983) aims to predict the conditions under which the biotic processes of competition and predation will be important determinants of community structure. The model was initially developed for marine intertidal communities (Connell 1975, Menge 1976, Menge and Sutherland 1976), and has since been applied to lotic communities (Peckarsky 1983, Walde 1986, Peckarsky et al. 1990, Lancaster 1996). The basic model proposes that predation is the principal process organizing community structure in physically benign environments. As the environment becomes harsher, the abundance and/or efficiency of predators is reduced and competition among prey becomes more important as their densities increase. In extreme environmental conditions, biotic processes become relatively unimportant and abiotic factors shape communities (Menge and Sutherland 1976, 1987, Peckarsky 1983).

Implicit in the prediction that increasing harshness will free prey from predation pressure is the assumption that the tolerance of prey to harshness exceeds that of predators (Connell 1975, Menge and Sutherland 1976, Underwood and Denley 1984, Walde 1986). In intertidal systems, Menge and Sutherland (1976) argued that sessile prey would be forced to endure severe conditions and should therefore evolve greater tolerance to a broader range of conditions than mobile predators, which, they argued, can simply leave harsh environments. In lotic habitats, the majority of fauna are highly mobile irrespective of trophic role (mobility may be an adaptation to unstable substrata and frequent hydrologic disturbance, Lake 1990, Mackay 1992, Townsend and Hildrew 1994). Thus an underlying premise of the original model does not seem to apply to lotic systems. Nevertheless, the harsh–benign hypothesis has frequently been applied to lotic habitats (Peckarsky 1983, Walde 1986, Allan 1995, Lancaster 1996) without alternative explanation of why differential tolerance to disturbance between predators and prey is expected.

Models that predict that the intensity or outcome of biotic interactions depend upon environmental conditions have been termed ‘‘environmental stress models’’ (ESMs; Menge and Olson 1990), of which there are two basic categories: ‘‘consumer stress models’’ (CSMs) and ‘‘prey stress models’’ (PSMs). CSMs pre-

---

Manuscript received 28 August 2000; revised 28 March 2001; accepted 9 April 2001.

[3] Present address: Patrick Center for Environmental Research, Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103 USA. E-mail: thomson@acnatsci.org

dict that predators will be more adversely affected by stressful conditions than will prey, and that predator impacts will therefore decline as environmental harshness increases. PSMs predict that abiotic harshness will weaken prey defences more than it will reduce predator efficiency, and that predator impacts will therefore increase with increasing harshness (Menge and Olson 1990, Kiffney 1996).

To render Environmental Stress Models falsifiable, it is necessary to clearly define several terms that have assumed variable meanings in the ecological literature: disturbance, perturbation, stress and harshness. A disturbance occurs when damaging forces are applied to habitat space occupied by a population, community, or ecosystem (Lake 2000). The effect of disturbance on the biota is defined as the response (Glasby and Underwood 1996, Lake 2000). The combination of cause (disturbance) and effect (response) is defined as perturbation (Glasby and Underwood 1996, Lake 2000). Stress is a type of response, specifically the physiological response of an individual, or the functional response of a system, to disturbance (Rykiel 1985). In summary, we define ‘‘abiotic disturbance’’ as the application of a damaging physical factor to the habitat of a population, community, or ecosystem. This includes any abiotic factor that causes physiological stress to organisms but does not necessarily reduce the number of individuals.

In adapting the harsh–benign hypothesis to streams, Peckarsky (1983:317) defined ‘‘harsh’’ as ‘‘a set of physical–chemical conditions that impose physiological problems [i.e., stress] for many stream invertebrates.’’ Thus ‘‘harsh’’ is essentially equivalent to ‘‘abiotic disturbance’’ as defined above, and ‘‘benign’’ is the absence of abiotic disturbance.

To clarify, we consider the harsh–benign hypothesis to be a consumer stress model (Menge and Sutherland 1987, Menge and Olson 1990); that is, it predicts that abiotic disturbance reduces the impact of predation within lotic communities by having more deleterious effects on predator populations than on prey populations.

One of the most common forms of natural abiotic disturbance in streams is flooding. Extreme elevations in discharge can result in severe shear forces that move substratum materials, scour and abrade the stream bed, remove plants and organic matter, and kill, injure, or displace biota (Resh et al. 1988, Lake 2000). Many studies have shown that floods can cause significant reductions in the populations of stream biota (Fisher et al. 1982, Brooks and Boulton 1991, Anderson 1992, Boulton et al. 1992, Flecker and Feifarek 1994, Matthaei et al. 1996, Miller and Golladay 1996).

There have been few previous attempts to examine the effects of abiotic disturbance on lotic predator impacts, and very few of these have involved flood disturbance. Results of those studies that have examined the effects of floods on predator impacts (Meffe 1984, Lancaster 1996) have provided inconclusive support for the harsh–benign hypothesis. Lancaster (1996) observed the predicted decline in predator impact with increasing disturbance intensity for only one of two predatory taxa investigated. Meffe (1984) found that frequent flooding reduced the impact of introduced mosquitofish on native topminnows because the introduced species lacks innate behavioral mechanisms for surviving floods. While this supports the harsh–benign hypothesis, the predator is an exotic and may be expected to be less adapted to local conditions, irrespective of its trophic role. Abiotic disturbances other than floods, including sedimentation and anthropogenic contaminants, have been found to reduce (Kiesecker 1996), increase (Clements et al. 1989), or have variable effects (Walde 1986, Kiffney 1996) on lotic predator impacts, casting doubt on the generality of Environmental Stress Models.

Disturbances may have indirect effects on predator impacts, such as removal of refugia, or may mask or reset the effects of predation by redistributing predators and prey (Power et al. 1985, Power 1990). Such effects may produce outcomes that superficially match the predictions of ESMs (e.g., reduced measurable predator impact). However to support ESMs, any change in predator impact must result from a change in the frequency or outcome of predator–prey interactions caused by differential tolerance to disturbance. Thus it is important to investigate the mechanism of any change in predator impact associated with disturbance.

This study aimed to test experimentally the hypothesis that extreme variation in flow would reduce the impact of a predatory stonefly, *Cosmioperla kuna*, on its prey. An experiment was conducted in open-ended stream channels that allowed prey migration, and both consumption and changes in prey emigration were measured, as well as final prey and predator densities, in order to determine the mechanisms of any differences in predator impact.

METHODS

Study site

All experiments were conducted within a 1-km stretch of the lower reaches of the Cumberland River, in southeastern Australia, ~200 km southwest of Melbourne, Victoria. The Cumberland River drains the southern slopes of the Otway Ranges, occupying a catchment area of 37.5 km^2. Mean annual discharge (gauged 200 m downstream of the experimental reach) is 0.76 m^3/s and bank-full discharge in the study reach is estimated at 4.63 m^3/s, which is exceeded on average 2.6 times per year (Theiss Environmental Services Propriety Limited [Melbourne, *Victoria, Australia*], *unpublished discharge data*). Floods are associated with rainstorms and may occur at any time of year. In the study reach, the river ranges from 5 to 8 m wide, and

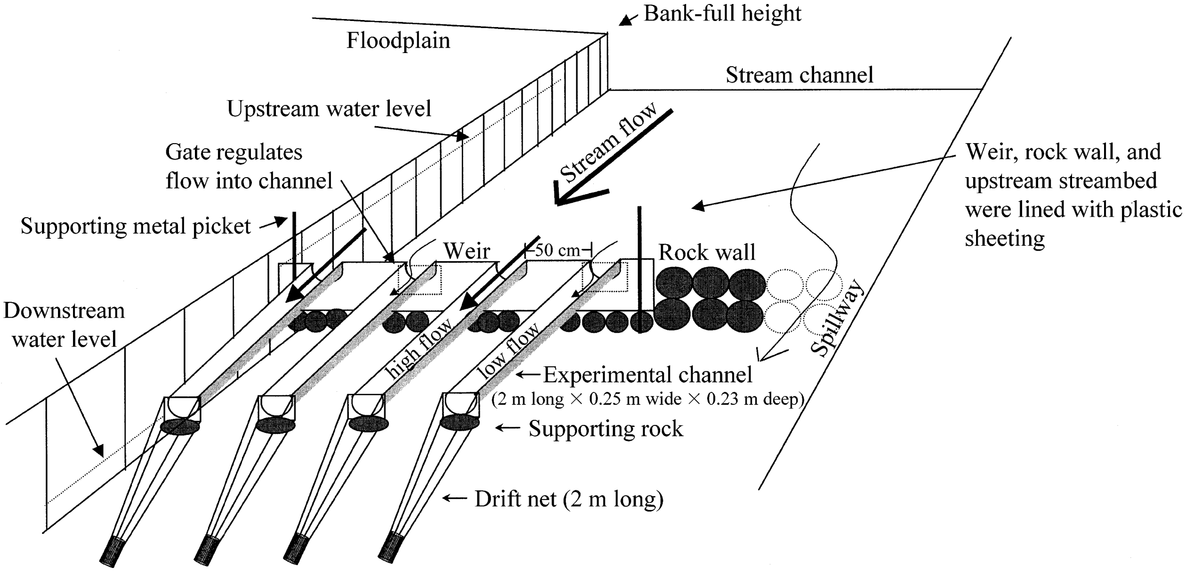

FIG. 1. Diagram of experimental stream channels. Flow into each channel was independently regulated by adjusting the height of acrylic gates (or removing them completely for maximum flow). Adding or removing rocks and/or plastic lining from the rock-wall extension regulated the proportion of total stream flow directed into the channels.

ranges in maximum depth from 0.3 m in riffles to 1.5 m in pools at base flow.

Study organisms

Cosmioperla kuna (formerly *Stenoperla australis*, McLellan 1996) is a eusthiniid stonefly common throughout the east coast of mainland Australia. The nymphs inhabit stony streams and are omnivorous, with mayfly and chironomid larvae generally constituting the bulk of the diet (Sephton and Hynes 1983, Vazquez 1998). The life cycle is believed to take between 1 and 3 yr (Hynes and Hynes 1975), and nymphs are present in the stream throughout the year. Nymphs reach up to 27 mm in length. *Cosmioperla* are abundant in the Cumberland River (average density in runs from October 1994 through March 1996 = 20 individuals/m^2) and prey mainly on the most abundant benthic invertebrates in the system: leptophlebiid and baetid mayflies, and chironomid larvae.

Experimental design and field protocols

A randomized complete-block design was used to examine the effect of *Cosmioperla* on densities and drift rates of its major prey under constant- and variable-flow conditions in artificial stream channels. Main treatment factors were Predators (present/absent) and Flow (constant/variable). Four channels were used in each block, with one channel per treatment. Each block was conducted at a different site within the 1-km stretch of river, and treatments were randomly assigned to channels for each block. Each block ran for 1 wk. The experiment was conducted twice in consecutive years, with three blocks in summer–autumn 1995 (conducted from February through early April) and four in spring–summer 1996 (October through December). A fourth block in 1995 was not included in analyses as a natural spate at that time increased flows and turbidity in all channels. To increase the power of analyses and examine any variation between years, results from the two groups of experiments were combined with Year (1 or 2) included as a factor in the analysis. The blocking factor (Block) was nested within Year.

Experimental channels.—Experiments were conducted in four, 2-m long, parallel stream channels (Fig. 1). Channels were constructed by cutting 2-m lengths of 250-mm diameter polyvinyl chloride pipe longitudinally in half (Brooks 1998). Rectangular strips (3 × 100 × 2000 mm) of transparent acrylic were attached to both sides of the resultant half pipes to extend the vertical sides of channels while minimizing shading. Each channel had a U-shaped cross-section 250 mm wide by 225 mm deep. A 50-mm high acrylic step was screwed into the downstream end of each channel to maintain a minimum depth at low flows.

A portable timber weir (0.5 m × 3 m × 30 mm) with four U-shaped notches cut into it (50 cm apart) was used to hold channels in place and to create high flows in channels. Metal fencing pickets and rocks were used to hold the weir partially immersed perpendicular to the current. The weir was extended laterally to the riverbanks with a rock wall. The resultant dam was lined with plastic to further impede flow. The rock wall could be partially dismantled to reduce flow through the channels if necessary.

The upstream end of each channel sat in one of the notches in the weir and the downstream end was supported by stream rocks. The bottom of each channel was at least 25 cm from the streambed, and channels sloped 4° downstream. A piece of acrylic sheeting (300 × 300 mm) at the upstream end of each channel could be raised or lowered to regulate flow through each channel independently (Brooks 1998). This gate was held in place by the pressure of the dammed water.

Substrata in the channels consisted of rocks (longest axis: between 5 and 20 cm) collected from the Cumberland River. Rocks were gently washed free of all animals before being placed into the channels with their original top surfaces with algae remaining uppermost. Rocks were arranged so that they would not be dislodged by high flows. A coarse mesh (1-cm^2 holes) fence was erected ~50 cm upstream of the weir to prevent fish and large debris from entering the channels.

Colonization.—The channels were left for two days at base-flow conditions (mean current velocity 1 cm above rock surface = 30 cm/s, depth = 5 cm) to allow colonization by invertebrates. Because the mouth of the channels was 25 cm from the riverbed, and the weir and bottom of its upstream ''pool'' covered in plastic, colonization was almost entirely by drifting animals. This was a deliberate strategy to allow prey immigration while restricting predator immigration. It was not possible to use mesh to prevent immigration of predators because they are similar in size to prey and restricting prey immigration may influence predator impacts (Cooper et al. 1990, Sih and Wooster 1994, Englund and Olsson 1996, Englund 1997). Also, mesh would have reduced the ability to create high flows in channels. However, a pilot experiment demonstrated that large *Cosmioperla* did not enter drift nets placed 20 cm above the streambed (four drift nets placed 20 cm above the substratum over five 24-h periods yielded a total of only two early instar and one late-instar *Cosmioperla*). It was therefore assumed that few if any large *Cosmioperla* would drift into channels during the experiment. In fact, a total of four early instar and two late-instar *Cosmioperla* were found in designated predator-free channels over all seven blocks. This method was therefore deemed successful in maintaining at least high vs. very low predator-density treatments.

The advantage of allowing prey immigration was considered to outweigh any possible unrealism of the channel assemblage lacking taxa that do not readily colonize via drift. *Cosmioperla*'s major prey, baetid and leptophlebiid mayflies, are common in the drift, and readily colonized the channels. A third common prey taxon, chironomid larvae, was rare in channels relative to its abundance in the natural stream. While it is conceivable that this would increase predation pressure on mayflies, this would have been the case in all treatments and so should not confound treatment comparisons.

Experimental protocol.—On the third day after channels were set up (day 1 of experiment) designated predator treatments were each stocked with 10 late-instar *Cosmioperla*, which were collected from the surrounding stream and placed immediately into channels. This corresponds to a density of 20 *Cosmioperla*/m^2, equivalent to average densities for the Cumberland River (Thomson 1999). Drift nets (250-μm mesh, 2 m long) were placed at the downstream end of channels prior to predator stocking.

Drift samples were collected over 24-h periods (long nets and coarse mesh upstream of channels prevented clogging) from day 2 to day 8; nets were cleared at 0900 each day. Downstream drift nets were checked for *Cosmioperla* after the first 3 d and any predators that had left channels were replaced with fresh individuals collected from the river on that day. This ensured a relatively high density of predators were present when the first flood started. From days 4 to 7, drifting predators were not replaced, as reduced densities due to drift may be a natural consequence of floods.

On days 2 and 3, 30-cm long, 250-μm nets were placed at the upstream end of channels for 45 min from 2030 to estimate incoming drift. Invertebrate drift rates vary with time of day and from day to day (Brittain and Eikeland 1988) and so these values cannot give an accurate measure of total drift into the channels. However, they do allow comparisons between channels to ensure treatments were not receiving different numbers of potential colonists. It was not possible to measure incoming drift during high flows because water backed up in the nets, reducing flow into the channels.

Between 0900 and 1300 on day 4 flow was gradually increased in the two variable-flow channels (one with and one without predators) up to maximum flow (>100 cm/s 1 cm above rocks, 20-cm depth). Between 0800 and 1200 on day 5 flow in these channels was gradually returned to base flow levels (30 cm/s). Current velocity was measured with a Nixon Streamflo [Nixon Flowmeters Limited, Cheltenham, UK] current meter 1 cm above five randomly chosen rocks in each channel with downstream drift nets in place. The flow was increased again on day 6 and returned to base flow on day 7.

Natural floods of moderate intensity in the Cumberland river typically last only 24–48 h but sometimes have a second peak 24–72 h after the first (*unpublished discharge data*, Theiss Environmental Services), so the use of two experimental floods within one week was not unrealistic, and allowed contrasting physical conditions to be maintained in constant- vs. variable-flow treatments over much of the one-week experiment.

Current velocity (1 cm above five random rocks) and water depth were measured daily and channel inlets adjusted to maintain an average velocity of ~30 cm/s (1 cm above rock surface) and depth of 10 cm to the channel floor (~5 cm to rock surface) in base-flow channels. On flood days (days 4 and 6), variable-flow channels were maintained at maximum depth (20 cm) and current velocity (current velocity within flooding channels was highly variable in space and time but peaks often exceeded 150 cm/s 1 cm above rock surfaces).

The experiment was terminated at 0900 on day 8. Fine nets were placed at the upstream end of each channel to prevent animals from drifting into channels. Final densities were determined by thoroughly washing all rocks and channel surfaces into clean nets at the downstream end of channels. All samples were preserved in 5% formalin solution and returned to the laboratory for sorting.

Laboratory procedures

Final benthic samples were sorted in their entirety, but the 24-h drift samples were subsampled to 20% using a Marchant (1989) subsampler. All *Cosmioperla* were removed from drift samples (by inspecting each of the 100 subsampler cells) prior to random selection of 20 cells for processing. Benthic samples and drift subsamples were washed through a series of nested sieves (mesh sizes 4.0 mm, 1.4 mm, 1.0 mm, and 0.01 mm). The contents of each sieve were placed into a sorting tray and examined under a Leica MZ6 dissecting microscope at 16× magnification (Leica, Solms, Germany). All animals were identified to species level and counted.

Gut contents.—*Cosmioperla* that remained in channels until at least day 4 were retained for gut-content analysis. Head widths were measured with a graticule. Animals were then dissected and gut contents mounted in Hoyer's solution. Slides were examined under 400× magnification and prey items identified to the lowest possible taxonomic level using voucher slides and taxonomic keys. Where it was not clear how many individual prey were present the minimum possible number was recorded based on the number of head parts and appendages present. That is, up to six legs and one head from one species were assumed to be one individual prey item.

The majority of individuals used in the gut-content analysis must have been in channels for at least 3 d, usually much longer (up to 10 d). Hence it is unlikely that prey items found in guts were left over from prey captured before the experiment (Malmqvist and Sjöström 1980, Allan 1982).

Analysis

The only prey taxa present in sufficiently high numbers for analysis were the mayflies *Austrophlebioides pusillus* (Ephemeroptera: Leptophlebiidae) and baetid Genus 2 MV sp. 3 (Ephemeroptera: Baetidae, hereafter baetids). These taxa are the principal prey of *Cosmioperla* in the Cumberland River (Vazquez 1998).

Final prey densities and drift rates were analyzed using four-factor ANOVA with Predator (present or absent), Flow (constant or variable), and Year (1 or 2) as crossed fixed factors, and Block nested within Year. Year was treated as a fixed factor because experiments were run in only two consecutive years, which cannot be considered a random sample of time. Block was treated as a random factor (i.e., blocks conducted at random times within each year, and at random sites along the river). The denominator for calculation of the F ratio for the test of Year is the Block mean square. All other factors are tested against the Error mean square.

Prey drift data were averaged over flood days (days 4 and 6), base-flow days (days 3, 5, and 7), and summed over all days (days 3 to 7) for each species in each experiment.

Predator densities, predator drift, and gut-content data were analyzed with the above design but without a Predator effect. For gut-content analysis, replicates were channel averages (i.e., average number of each prey type found in predators from each channel) not individual predators.

Following significant interaction terms, specific contrasts were made only between treatments that shared a common level of one factor. Thus following a significant Flow × Predator interaction, the effects of predators in constant- and variable-flow treatments were examined separately, and the effect of flow regime in predator and predator-free treatments were also tested separately.

An index of per capita predator impact was calculated for *Cosmioperla*'s impact on *Austrophlebioides* and baetids in each experimental trial. Predator impact (PI) was calculated as the negative of the natural log of the ratio of the number of prey remaining in predator channels (N_p) to the number remaining in control channels (N_c) (Cooper et al. 1990, Sih and Wooster 1994). This figure was then divided by the mean number of predators in each channel (X) to give an estimate of per capita predator impact (PI/X) (Kratz 1996). The mean number of *Cosmioperla* in each channel (X) was calculated by estimating the number present for each of the final five days of the experiment and averaging these values. The number of *Cosmioperla* present in each channel on each day (P_n) was estimated as the average of the initial and final numbers for each 24-h period, which were calculated from initial predator densities (10 predators per channel) and daily drift rates:

$$\mathrm{PI}_{\mathrm{pred}} = \frac{\mathrm{PI}}{X}$$

with

$$\mathrm{PI} = -\ln\left(\frac{N_p}{N_c}\right)$$

$$X = \frac{\sum_{n}^{3,7} (I_n + F_n)/2}{5} = \frac{\sum_{n}^{3,7} (2I_n - D_n)/2}{5}$$

where N_p and N_c are the final numbers of prey in predator and predator-free (control) channels respectively, F_n and I_n are the final and initial numbers of predators on day n respectively, and D_n is the number of predators

TABLE 1. Results of ANOVA comparing the effects of flow regime and year on final *Cosmioperla* densities, *Cosmioperla* drift rates on flood days, and total *Cosmioperla* drift over all 7 days.

		Final density			Emigration on flood days			Total emigration		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
ANOVA results										
Year	1	5.720	1.318	0.303	1.570	1.699	0.249	<0.001	<0.001	0.996
Flow	1	11.010	6.319	0.054	3.793	6.878	**0.047**	1.361	1.822	0.235
Year × Flow	1	7.292	4.187	0.096	2.126	3.856	0.107	5.470	7.323	**0.042**
Block(Year)	5	21.708	2.493	0.169	4.621	1.676	0.292	24.317	6.510	**0.030**
Error	5	8.708			2.757			3.735		
Specific contrasts†										
Y_1 con. vs. Y_1 var.								0.601	0.805	0.411
Y_2 con. vs. Y_2 var.								7.169	9.596	**0.027**
Y_1 var. vs. Y_2 var.								2.710	3.627	0.115
Y_1 con. vs. Y_2 con.								2.761	3.696	0.113
Error								3.735		

Notes: Specific contrasts were performed to detect differences between treatment combinations following significant Year × Flow interaction for total emigration. Boldface *P* entries indicate significance at $P < 0.05$.

† Y_1 = Year 1, Y_2 = Year 2; con. = constant flow, var. = variable flow.

drifting out of channels over day *n* (24-h period). $I_3 = 10$.

Each of the response variables analyzed provides different information and aids in interpretation of the overall results, and is therefore worthy of separate analysis despite potential interdependence between some variables (Huberty and Morris 1989). Because we were interested in the response of each variable to treatments we followed the recommendation of Huberty and Morris (1989) and conducted multiple ANOVA without preliminary MANOVA. Assumptions of ANOVA were checked by examining both Box and residual plots. Where necessary, response variables were transformed (square root or $\log(n + 1)$) to ensure homogeneity of variances.

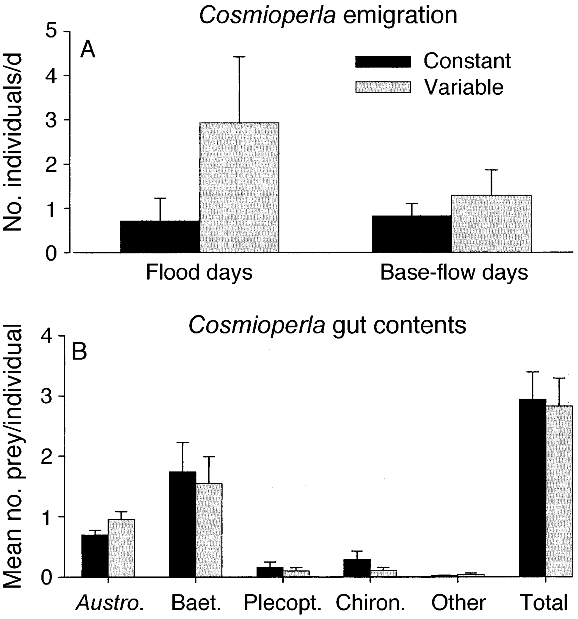

FIG. 2. *Cosmioperla* results. (A) Emigration (mean and 1 SE) on flood and base-flow days. (B) Number of prey items (mean and 1 SE) found in guts of *Cosmioperla* from constant- and variable-flow channels. Mean number of prey for each treatment was calculated from channel averages; *Austro.* = *Austrophlebioides*, Baet. = baetids, Plecopt. = Plecoptera, Chiron. = chironomids. $N = 7$ channels for all bars.

RESULTS

Flood effects on predators

Final *Cosmioperla* densities were not significantly different between variable-flow channels (2.71 ± 0.89 individuals [mean ± 1 SE]) and constant-flow channels (4.57 ± 1.08 individuals) ($P = 0.054$, Table 1), despite a trend for lower densities in variable-flow treatments. However, the average rate of predator emigration was significantly higher during floods ($P = 0.047$, Table 1, Fig. 2A), and, in the second year, total predator emigration over all days was significantly higher from variable-flow channels than from constant-flow channels (Table 1).

There were no significant differences between the number of prey items found in predator guts from constant- and variable-flow channels for any prey group or for the total number of prey (Table 2, Fig. 2B). Predators in both flow treatments consumed significantly fewer baetids ($P = 0.024$, Table 2) and significantly more plecopterans ($P = 0.005$, Table 2) in the second year than in the first (baetids, Year 1 = 2.62 ± 0.49 individuals [mean ± 1 SE], Year 2 = 0.90 ± 0.14 individuals; Plecoptera, Year 1 = 0.03 ± 0.03 individuals, Year 2 = 0.20 ± 0.08 individuals). This probably reflects the reduced number of baetids in the channels in 1996, which in turn reflects lower densities in the Cumberland River in 1996. The numbers of baetids and *Austrophlebioides* found in guts of experimental *Cosmioperla* were similar to those found in animals collected from the Cumberland River in 1995 and 1996 (Thomson 1999). Experimental *Cosmioperla* generally

TABLE 2. Results of ANOVA testing main and interactive effects of Flow and Year on *Cosmioperla* gut contents.

		Austrophlebioides			Baetids		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*
Flow	1	0.064	2.907	0.149	0.013	0.267	0.627
Year	1	0.002	0.046	0.839	1.475	10.336	**0.024**
Flood × Year	1	0.000	0.009	0.929	0.011	0.227	0.654
Block(Year)	5	0.173	1.582	0.314	0.714	2.992	0.127
Error	5	0.109			0.239		

Note: Boldface P entries indicate significance at $P < 0.05$.

had fewer chironomids but more small plectoptera and other drifting invertebrates (e.g., trichoptera) in their guts than field-collected *Cosmioperla*.

Predator, flow, and interactive effects on prey

Colonization of channels.—The number of baetids and *Austrophlebioides* drifting into channels (estimated with 45-min drift samples at channel entrances on days 2 and 3) were significantly greater (Table 3) in Year 1 (*Austrophlebioides* = 56.3 ± 4.7 individuals [mean ± 1 SE], baetids = 184.5 ± 16.5 individuals) than in Year 2 (*Austrophlebioides* = 29.6 ± 5.7 individuals, baetids = 60.3 ± 6.2 individuals), reflecting a general pattern of lower invertebrate densities in the Cumberland River in 1996 than in 1995. These differences in colonization rates resulted in many significant Year effects for mayfly densities and drift rates. However, there were no significant interactions between Year and any other factor for any dependent variable relating to mayflies.

There were no significant differences between treatments in the mean number of baetids or *Austrophlebioides* drifting into channels in the evenings of days 2 and 3 (Table 3). Incoming drift rates (i.e., potential immigrants) are therefore assumed to be equivalent for all treatments. It was not possible to measure incoming drift during floods, however it is assumed that if predator and predator-free treatments had equivalent immigration at base flow, and flows were increased by the same amount, then changes in drift into channels should be equivalent. Any predator effects, whether in constant- or variable-flow channels, are therefore attributed to the effects of predators, not to any differences in immigration rates between predator and predator-free channels.

Effects of predators and flow on prey densities.—Final *Austrophlebioides* densities (Fig. 3A) were significantly lower in variable-flow channels than in constant-flow channels ($P = 0.009$, Table 4) and significantly lower in predator channels than in predator-free channels ($P < 0.001$, Table 4). There was no interaction between the effects of predator and flow ($P = 0.799$, Table 4). Per capita predator impact (Fig. 3C) was not significantly different between constant- and variable-flow treatments ($P = 0.315$, Table 5).

There was a significant interaction ($P = 0.023$) between the effects of predators and flow on final baetid densities (Table 4, Fig. 3B). This was due to a significant effect of predators in variable-flow treatments but not in constant-flow treatments (Table 4). Baetid densities were lower in variable-flow channels with predators than in predator-free variable-flow channels (Fig. 3B). Per capita predator impact on baetids (Fig. 3C) was significantly higher in variable-flow treatments than in constant-flow treatments ($P = 0.048$, Table 5).

Prey Emigration.—Because it was not possible to estimate incoming drift during floods no conclusions can be drawn about the effects of floods on mayfly emigration (higher drift rates may simply indicate more animals drifting through channels). However, assuming the number of mayflies entering channels is equivalent within flow treatments (Table 3), comparisons of drift rates between predator and predator-free treatments provide information on the effects of predators on net mayfly emigration in constant- and variable-flow channels.

Total *Austrophlebioides* drift was significantly greater out of variable-flow channels with predators than out of variable-flow channels without predators and constant-flow channels with predators ($P = 0.033$, Table 6). These results were also reflected in analysis of mean drift on flood days (Table 6, Fig. 4A). There were no effects of predators on mean *Austrophlebioides* drift rates on base-flow days for either flow treatment (Table 6). Thus, predators significantly increased *Austrophlebioides* emigration during floods but not at base flow.

Total baetid drift was significantly higher from predator treatments than from predator-free treatments ($P = 0.045$, Table 7). The predator effect was evident on flood days ($P = 0.030$, Table 7, Fig. 4B), but not on base flow days ($P = 0.184$, Table 7). This suggests that baetid drift was higher from all predator channels but that the difference was relatively small at base flow and only detected when added to relatively large differences during floods. Baetid drift out of predator channels in flood was on average 51% greater than out of predator-free channels in flood, compared with predator effects of 19%, 14%, and 25% in constant-flow channels on flood days, constant-flow channels on no-flood days, and variable-flow channels on no-flood days, respectively. There was a marginally significant ($P = 0.05$) flow effect on baetid drift on normal-flow days (Table 7), suggesting some carryover effect of high flows on the following days' drift rates. This could be due to behavioral modifications (baetids leaving re-

TABLE 2. Extended.

Plecoptera			Chironomidae			Total		
SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
<0.001	0.002	0.965	0.135	0.924	0.381	0.003	0.268	0.626
0.292	21.968	**0.005**	0.019	0.564	0.487	0.623	4.943	0.077
0.072	0.607	0.471	0.010	0.069	0.803	0.004	0.304	0.605
0.066	0.113	0.984	0.171	0.234	0.931	0.630	9.761	0.013
0.590			0.732			0.065		

cently disturbed channels), or it could indicate that high flows increased immigration into channels, thereby increasing the source of emigrants on following days.

Comments on Block factor.—The Block factor was highly significant in all analyses of mayfly densities and drift. This indicates that there was considerable variation over time (as also indicated by significant Year effects) in the number of mayflies colonizing and drifting through channels (hence large error bars in Fig. 2–4). That significant treatment (Predator and Flow) effects and interactions between factors were attained demonstrates that these effects were strong in spite of variations in mayfly densities. This is confirmed by the lack of any significant interactions between Year and any other factor in analyses of mayfly densities and drift rates (dependent variables).

It was not possible to examine interactions between blocks and treatments, as each block had only one replicate of each treatment combination. The data from each block were examined to ensure that significant treatment effects reflected real patterns in the data. In all cases where significant differences between treatments were found, plots of treatment means against block were parallel, indicating that the treatment effect was the same in each block. Analysis results therefore reflect real patterns.

DISCUSSION

The results of this experiment are counter to predictions of the harsh–benign hypothesis. The reduced *Austrophlebioides* densities in, and increased *Cosmioperla* emigration from, variable-flow channels confirms that experimental floods constituted a disturbance to the faunal assemblage within channels. However, contrary to the predicted decline in predator impact, the impact of *Cosmioperla* on two of its major prey taxa was either unaffected (*Austrophlebioides*) or increased (baetids) by variations in flow.

The increased predator impact on baetids could be regarded as supporting prey stress models (PSMs), which predict that predator impacts will increase as environmental harshness increases (Menge and Olson 1990, Kiffney 1996). However, the mechanism of increased predator impacts proposed by PSMs is greater tolerance to disturbance among predators than prey, resulting in increased prey vulnerability to predation. Our results do not clearly support this prediction. According to PSMs, the increase in *Cosmioperla*'s impact on baetids should be explained by *Cosmioperla* having greater tolerance to floods than baetids. There is no evidence that this is the case, either from this study (no flow effect for baetids or *Cosmioperla* densities, but increased *Cosmioperla* emigration from flooding channels and trend for reduced *Cosmioperla* densities in flooded treatments), or from surveys of benthic populations following four natural floods in the Cumberland River (Thomson 1999). Furthermore, the effects of experimental floods in predator-free channels and the results of field surveys (Thomson 1999) both indicate that *Austrophlebioides* is less resistant to floods than baetids or *Cosmioperla*. If predator impacts are determined by relative tolerances, as predicted by

TABLE 3. Results of ANOVA testing differences in the rate of *Austrophlebioides* and baetid drift into treatment channels.

		Austrophlebioides			Baetids		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*
Year	1	3.987	7.612	**0.040**	7.935	40.26	**0.001**
Predator	1	0.583	1.099	0.311	0.004	0.012	0.915
Flow	1	0.025	0.047	0.831	0.274	0.800	0.385
Predator × Flow	1	0.276	0.520	0.482	0.003	0.009	0.925
Year × Predator	1	0.003	0.006	0.940	0.114	0.333	0.572
Year × Flow	1	0.028	0.053	0.821	0.081	0.237	0.634
Year × Pred × Flow	1	1.083	2.040	0.174	0.011	0.032	0.861
Block(Year)	5	2.619	0.987	0.458	0.985	0.576	0.718
Error	15	7.964			5.134		

Notes: Data used are averages of numbers caught in drift nets at channel entrances over two 45-min periods from 2030 on days 2 and 3. Boldface *P* entries indicate significance at $P < 0.05$.

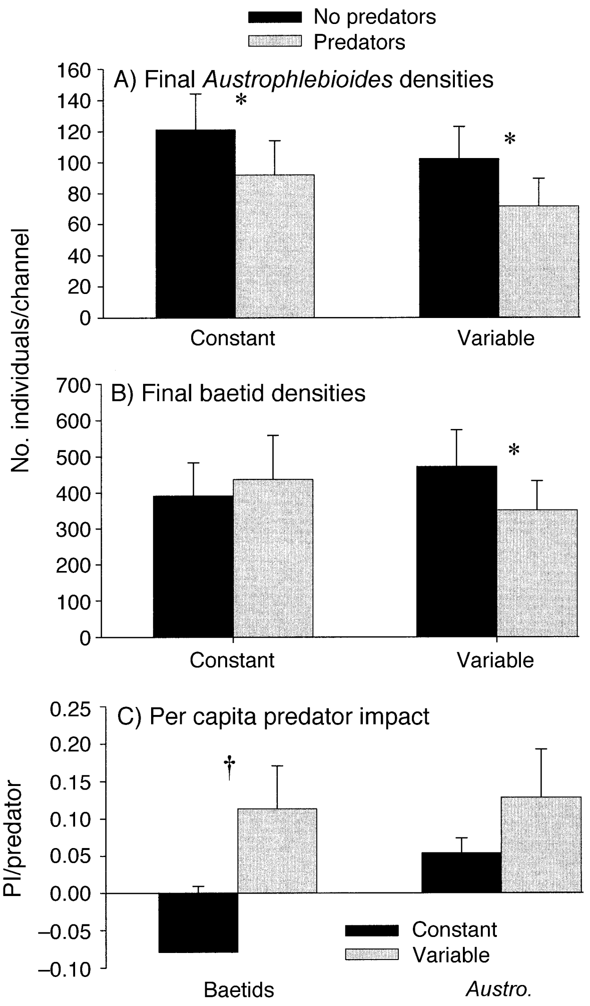

FIG. 3. Final prey densities for (A) *Austrophlebioides* and (B) baetids in constant- and variable-flow treatments, with and without predators. Data are means and 1 SE, $n = 7$ channels for all bars; asterisks (*) indicate a significant predator effect ($P < 0.05$) in ANOVA. For *Austrophlebioides* there was also a significant flow effect that was independent of predator presence. (C) Per capita predator impact (PI) on mayflies in constant- and variable-flow treatments. Data are means and 1 SE, $n = 7$ channels for all bars; the dagger (†) indicates a significant flow effect ($P < 0.05$) in ANOVA.

PSMs, then the greatest impact should fall on the least resistant prey. In fact the greatest increase in predator impact occurred on the most disturbance-resistant prey.

At least one reason for the discrepancy between the observed effects of disturbance on predator impacts and those predicted by environmental stress models (ESMs) appears to be the role of nonlethal predator effects. Previous investigations into the effects of disturbance on invertebrate predator–prey interactions have only considered changes in prey consumption (Walde 1986, Kiffney 1996, Lancaster 1996). Our results suggest that predator-induced emigration may also be important during disturbance.

Final predator densities were either unchanged or reduced in variable-flow channels, and gut-contents data provide no evidence of increased prey consumption in variable-flow treatments (Fig. 2B). Indeed, results of a behavioral study (Thomson 1999) show that foraging activity and consumption rates of *Cosmioperla* are reduced during very high flows. Thus the total number of prey consumed would at best remain constant, and probably decline in variable-flow treatments. Because final baetid densities were unaffected by floods and total consumption remained constant or declined, the proportion of baetids consumed did not increase. Therefore, the increased predator impact on this taxa is most likely the result of increased predator-induced prey emigration. Although there was no predator × flow interaction for baetid emigration, the fact that a predator effect was only detected on flood days suggests that the effect size was greater in flooding channels, that is, that floods increased predator-induced emigration (see also Fig. 4B).

For *Austrophlebioides* there was a definite increase in predator-induced emigration during floods (Table 6, Fig. 4A). This did not significantly increase predator impact, but it may have prevented a decline in predator impact. The significant reduction in final *Austrophlebioides* densities in all variable-flow treatments suggests that backgound *Austrophlebioides* emigration increased during floods. If background prey emigration increases, then predator impacts should decrease unless consumption rate (per capita of prey) or predator-induced emigration also increase (Sih and Wooster 1994). Given that total consumption probably declined in variable-flow treatments (as discussed above), it is likely that *Cosmioperla*'s impact on *Austrophlebioides* would have declined if predator-induced emigration had not increased during floods.

Increased predator-induced drift during floods could result from one or more of the following mechanisms: increased encounter rates between predators and prey; increased probability of prey entering the drift after encountering predators; or increased drift distances in high flow. Encounter rates between predators and prey may have increased during floods due to the active and/or passive movement of animals into low-flow refugia (Lancaster 1996). In this experiment, refugia may simply have been the underside of rocks (Brooks 1998, Thomson 1999), or there may have been certain areas within channels where shear stresses were lower than in surrounding areas (Davis and Barmuta 1989, Lancaster and Hildrew 1993). Contact with predators may have induced direct drift entry (e.g., Peckarsky 1980, Walton 1980, Malmqvist and Sjöström 1987, Williams 1987, Peckarsky and Penton 1989*a, b*) or caused prey to crawl (Peckarsky 1987, Peckarsky and Penton 1989*b*) out of refugia into areas where the probability of dislodgment was high due to increased shear stress (Hart and Merz 1998). Vazquez (1998) found that baetids tend to drift in response to *Cosmioperla*, whereas *Austrophlebioides* tend to crawl away. Thus, increased

TABLE 4. Results of ANOVA testing the main and interactive effects of Predators, Flow, and Year on final *Austrophlebioides* and baetid densities in stream channels.

		Austrophlebioides			Baetids		
	df	SS	*F*	*P*	SS	*F*	*P*
ANOVA results							
Year	1	113.517	12.633	**0.016**	851.695	30.276	**0.003**
Predator	1	17.168	21.847	<**0.001**	7.810	1.852	0.194
Flow	1	7.154	9.103	**0.009**	0.010	0.002	0.962
Predator × Flow	1	0.053	0.067	0.799	26.889	6.378	**0.023**
Year × Predator	1	0.078	0.099	0.758	2.498	0.593	0.453
Year × Flow	1	0.004	0.005	0.942	4.485	1.064	0.319
Year × Pred × Flow	1	0.036	0.046	0.833	5.193	1.232	0.285
Block(Year)	5	44.93	11.435	<**0.001**	140.655	6.672	**0.002**
Error	15	11.787			63.243		
Specific contrasts†							
N, con. = N, var.					12.937	3.068	0.100
P, con. = P, var.					13.962	3.312	0.089
N, con. = P, con.					2.858	0.678	0.423
N, var. = P, var.					31.841	7.552	**0.015**
					63.243		

Notes: Specific contrasts were performed to detect differences between treatment combinations following significant Predator × Flow interaction for baetids. Boldface *P* entries indicate significance at $P < 0.05$.

† N = no predators, P = predators; con. = constant flow, var. = variable flow.

encounter rates in flow refugia would probably increase the incidence of active drift entry by baetids and passive drift entry by *Austrophlebioides*.

Higher flows would increase the distance prey travel while in the drift and therefore may have increased the number of mayflies entering drift nets even if encounter rates with predators were not higher during floods. However, behavioral experiments (Thomson 1999) showed that *Cosmioperla* spend significantly more time under rocks during high flows, so unless some prey also moved under rocks encounter rates (and therefore drift entry) would decline. It is therefore unlikely that the differences in drift rates could be explained solely by increased distances travelled once prey entered the drift. Nevertheless, the increased distances prey would drift during floods would add to the dispersal of prey from predator patches.

Increased predator-induced drift during floods would be most likely to increase predator impacts if the prey's normal response to high flows was to reduce drift and seek refuge. In this case emigration from predator-free patches in which refugia were available would decrease during floods, but emigration from predator patches may increase. Note however that even if background prey emigration increased during floods, predator impacts could still increase as a result of predator induced emigration, as long as the rate of predator-induced emigration increased faster than the rate of background emigration (Sih and Wooster 1994). This is possible if the concentration of predators and prey in refugia during disturbance led to a large increase in encounter rates, and/or if the likelihood of prey entering the drift, and the distance they travel in the drift, increased during disturbance.

Realism of results and the question of scale

The responses of organisms to small-scale experimental disturbances are not always consistent with responses to large-scale disturbance events (Brooks and Boulton 1991, Matthaei et al. 1997). Two factors potentially reduce the realism of experimental floods: the fact that channel substrata were relatively stable during floods (although some rocks did move), and the lack of a hyporheic zone. However, observations after real

TABLE 5. Results of ANOVA testing differences between per capita predator impact (PI/*X*) on *Austrophlebioides* and baetids in constant- vs. variable-flow channels.

		Austrophlebioides			Baetids		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*
Year	1	0.008	0.525	0.501	0.014	0.268	0.627
Flow	1	0.023	1.245	0.315	0.156	6.810	**0.048**
Year × Flow	1	0.009	0.514	0.506	0.074	3.234	0.132
Block (Year)	5	0.080	0.865	0.561	0.261	2.279	0.193
Error	5	0.092			0.115		

Notes: Details of the calculation of PI/*X* are given in the text (see *Methods: Analysis*). The boldface *P* entry indicates significance at $P < 0.05$.

TABLE 6. Results of ANOVA testing differences in *Austrophlebioides* drift on flood days, normal-flow days, and over the whole experiment.

		Total drift			Drift on flood days			Drift on normal flow days		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
ANOVA results										
Year	1	15.544	9.464	**0.028**	10.87	3.88	0.106	19.477	16.473	**0.010**
Predator	1	0.043	0.478	0.500	0.094	0.618	0.445	0.000	0.001	0.976
Flow	1	0.425	4.741	**0.046**	0.895	5.907	**0.029**	0.023	0.136	0.718
Predator × Flow	1	0.495	5.524	**0.033**	1.472	9.715	**0.008**	0.072	0.426	0.524
Year × Predator	1	0.169	1.888	0.190	0.063	0.419	0.528	0.379	2.236	0.156
Year × Flow	1	0.072	0.800	0.385	0.189	1.248	0.283	0.676	3.991	0.064
Year × Pred × Flow	1	0.058	0.644	0.435	0.000	0.002	0.968	0.436	2.571	0.130
Block(Year)	5	8.212	18.335	<**0.001**	14.007	18.487	<**0.001**	5.912	6.976	**0.001**
Error	15	1.344			2.121			2.542		
Specific contrasts†										
N, con. = N, var.	1	0.001	0.015	0.904	0.037	0.247	0.627			
P, con. = P, var.	1	0.918	10.25	**0.006**	2.23	14.718	**0.002**			
N, con. = P, con.	1	0.123	1.376	0.259	0.431	2.846	0.114			
N, var. = P, var.	1	0.414	4.626	**0.048**	1.104	7.284	**0.017**			
Error	15	1.344			2.121					

Notes: Specific contrasts were performed to detect differences between treatment combinations following significant Predator × Flow interaction for total drift and drift on flood days. Boldface *P* entries indicate significance at $P < 0.05$.

† N = no predators, P = predators; con. = constant flow, var. = variable flow.

floods and estimation of critical shear stresses suggest that much of the substratum in the Cumberland River remains stable during moderate-size floods, which may nevertheless significantly reduce benthic densities (Thomson 1999). Floods may still impose a physical disturbance to stable patches because high shear stresses can remove macroinvertebrates from stable substrata (Bond and Downes 2000). None of the taxa in this experiment are morphologically suited to burrowing nor have they been observed to use the hyporheic zone as a refugium (e.g., Marchant 1988), so the lack of a hyporheic zone probably did not reduce effective refuge space available to predators or prey. The effects of experimental floods on baetid, *Austrophlebioides*, and *Cosmioperla* densities were consistent with the observed effects of real floods in the Cumberland River (Thomson 1999). It therefore seems reasonable to extrapolate the results of these predator-impact experiments to natural floods, at least to patches in which there is little substratum movement. The degree of substratum movement at a given discharge may be highly variable within and between rivers (Downes et al. 1998), and in many streams there will often be at least some areas in which the substratum is stable during disturbance.

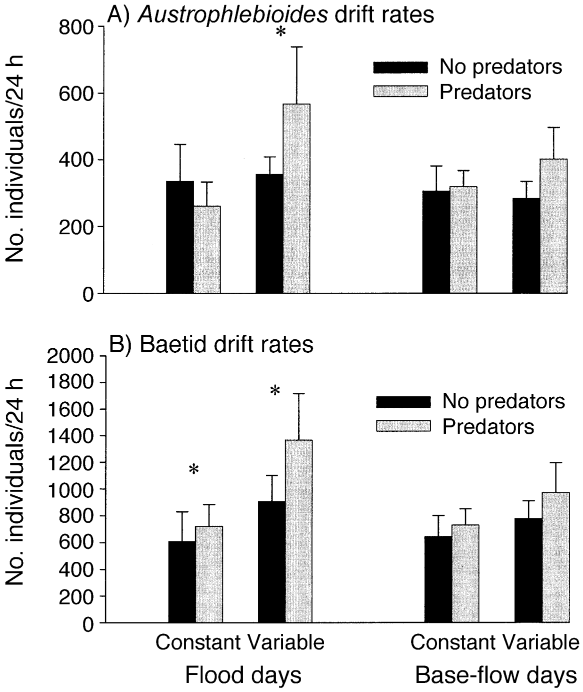

FIG. 4. Drift rates on flood and base-flow days for (A) *Austrophlebioides* and (B) baetids in predator and predator-free channels. Data are means and 1 SE, $n = 7$ channels for all bars, and asterisks (*) indicate significant predator effects ($P < 0.05$) in ANOVA.

Whether increased predator impacts in small-scale patches of stable substratum during floods would affect populations at larger scales remains an important question (Lancaster 1996, McPeek and Peckarsky 1998), one that requires larger-scale studies to answer. However it is worth noting two factors that may make our results relevant to larger scales. First, predator-induced dispersal during disturbance may have larger-scale impacts on prey densities than predator avoidance under normal flow conditions. Under normal conditions, prey that escape from predators may only travel short distances, and are therefore likely to remain within larger areas (Englund 1997). However, prey that escape predators during floods may be carried large distances by rapid currents (Anderson and Lehmkuhl 1968, Elliot 1971, Ciborowski 1983, Allan and Feifarek 1989, Lan-

TABLE 7. Results of ANOVA testing differences in baetid drift on flood days, normal flow days, and over the whole experiment.

		Total drift			Drift on flood days			Drift on normal flow days		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Year	1	36.939	36.381	**0.002**	33.623	32.060	**0.002**	41.587	33.242	**0.002**
Predator	1	0.468	4.806	**0.045**	1.053	5.735	**0.030**	0.208	1.939	0.184
Flow	1	1.439	14.768	**0.002**	2.780	15.136	**0.001**	0.485	4.527	0.050
Predator × Flow	1	0.021	0.218	0.648	0.019	0.106	0.749	0.023	0.210	0.653
Year × Predator	1	0.007	0.067	0.799	0.006	0.035	0.855	0.006	0.053	0.822
Year × Flow	1	0.011	0.111	0.743	0.084	0.460	0.508	0.049	0.460	0.508
Year × Pred × Flow	1	0.022	0.227	0.641	0.006	0.032	0.861	0.039	0.367	0.553
Block(Year)	5	5.077	10.418	<**0.001**	5.244	5.709	**0.004**	6.255	11.668	<**0.001**
Error	15	1.462			2.755			1.608		

Note: Boldface P entries indicate significance at $P < 0.05$.

caster et al. 1996), or be killed or injured by tumbling rocks or debris. Second, if, as is generally presumed (Death and Winterbourn 1995, Townsend et al. 1997, Downes et al. 1998), population losses during floods are greater where the substratum is not stable, then interactions within stable patches may involve a large proportion of surviving individuals. If surviving prey are concentrated in stable patches (either through active refuge seeking or because survival is higher in those patches), then predator impacts in those patches may have a large influence on the overall population of a larger area (particularly if escaping prey are carried out of that area or killed).

Generality of environmental stress models

The results of this experiment contradict consumer stress models (CSMs), because predator impacts increased or remained constant with disturbance, and also contradict prey stress models (PSMs) because changes in predator impacts were not a simple function of the relative tolerances of predator and prey taxa to disturbance. Other studies (Walde 1986, Wallace et al. 1987, Kiffney 1996, Lancaster 1996) of the effects of disturbance (or harshness) on lotic predator impacts have shown similarly complex results, with no simple relationships between disturbance intensity and predator impacts on all prey.

Lancaster (1996) found that the effects of floods on prey consumption rates of invertebrate predators varied between taxa and between different microhabitat patch types. For *Plectrocnemia conspersa*, consumption rates were higher in patches identified as low-flow refugia during high flow, but unchanged in other patch types. For *Sialis fuliginosa*, consumption rates were unchanged in low-flow patches during disturbance, but reduced in other patch types. These results support the possibility that encounter rates increase in flow refugia during floods. Using a model that accounts for spatial heterogeneity, Lancaster (1996) calculated that net predator impacts at the reach scale would decrease with increasing hydraulic disturbance for *S. fuliginosa*. However, there was no directional trend for *P. conspersa*, which may have had maximum impact at intermediate-disturbance levels. These estimates of predator impact (PI) were based on gut contents of predators and so do not account for prey migration, which could increase the overall effect of predators on prey abundance within patches, and at the reach scale if drifting prey are carried out of the reach by high flows.

Walde (1986) found that increased sediment levels could lead to either an increase or a decrease in the impact of a predatory stonefly (*Kogotus nonus*), depending on the coarseness of the sediment. In common with Lancaster's (1996) study, predation impact was not a linear function of disturbance intensity, because predator impacts were highest at intermediate disturbance intensity (i.e., in coarser-sediment treatments that had little effect on prey or predator densities). Walde's (1986) study demonstrates that even small differences in disturbance type (size distribution of sediment particles) can result in very different effects on predator–prey interactions.

Kiffney (1996) found that heavy-metal contamination increased the impact of a predatory stonefly, *Hesperoperla pacifica* (Plecoptera: Perlidae), on hydropsychid caddisflies, and in this case previous studies had demonstrated that the predator was more tolerant of heavy metals than its prey (Kiffney 1996). Thus Kiffney (1996) concluded that his results supported PSMs. However there was one result that was contrary to PSMs. *H. pacifica*'s impact on a stonefly prey species (*Prostoia besametsa*) decreased in metal-dosed treatments. *P. besametsa* was the only species in the experimental system whose density was reduced by the heavy-metal treatment, and Kiffney (1996) attributed the reduced predator impact on this prey to its reduced density in metal-treated microcosms. Thus the least resistant prey taxa, which was much less resistant to heavy metals than the predator, experienced the lowest impact of predation. This example highlights a major difficulty of using relative tolerances to disturbance to predict predator impacts. If prey have very low tolerance to a particular disturbance then their density may be so reduced that predators cannot or do not prey upon them, irrespective of the effect of that disturbance on the predator (Walde 1986, Peckarsky et al. 1990). This will be particularly so if alternative prey are available.

Peckarsky et al. (1990:189) proposed the confounding effects of prey density on predator impacts as one reason why ''one cannot predict with confidence the relative impact of predators on prey populations along a continuum of abiotic conditions perceived by prey as harsh to benign,'' but suggested that predator impacts could be predicted solely on the basis of the predator's reactions to abiotic conditions. However, the effects of disturbance on prey can affect predator impacts, whether by influencing the vulnerability of prey (Underwood and Denley 1984, Walde 1986, Clements et al. 1989, Kiffney 1996), or, as Peckarksky et al. (1990) argue, by reducing their density so that they become unavailable. Therefore the predator's response to the environment alone cannot be sufficient to predict predator impacts. Indeed, there are several examples of predator impacts increasing due to a disturbance that does have some detrimental effect on predators (e.g., Kiffney 1996, Lancaster 1996, Walde 1986, this study).

Clearly the responses of both predator and prey to disturbance are important, but there will not necessarily be a simple relationship between their relative tolerances and predator impacts. Disturbances may influence predator impacts by affecting factors other than the relative density or physiological condition of predators and prey. Indirect effects such as the accumulation of fauna in disturbance refugia, altered prey exchange rates, removal of predation refugia (e.g., macrophytes), and changes in the relative abundances of alternative prey (or predators) could all interact with the direct effects of disturbance to determine a predator's impact on its prey.

Further complicating the prediction of predator impacts are indirect predator effects, which have received little, if any, consideration in the formulation and testing of Environmental Stress Models (ESMs). Predators have many nonlethal effects on prey under ''normal'' environmental conditions (Cerri and Fraser 1983, Peckarsky et al. 1993, Peckarsky and Cowan 1995, Peckarsky 1996), and these often interact with other factors to influence prey fitness and abundance (Dill 1987, Lima and Dill 1990, Soluk and Richardson 1997, McPeek and Peckarsky 1998, Peckarsky and McIntosh 1998, Sih et al. 1998). There is little reason to assume that predators will not also influence the behavior and distribution of their prey during disturbance. Whatever the prevailing abiotic conditions, organisms must eat and avoid being eaten, and innate behaviors associated with these needs will not necessarily be suppressed during disturbance. Therefore nonlethal predator effects may still operate during disturbance, and these may interact with the disturbance to influence prey survival and fitness. Predator escape or avoidance responses are widespread in aquatic and terrestrial biota (Kerfoot and Sih 1987, Lima and Dill 1990, Sih et al. 1998), and these may have particularly important effects during disturbance, because prey that leave refugia in response to predators may be subjected to hazardous physical conditions.

Conclusion

Our results provide no support for the harsh–benign hypothesis (CSMs) and are inconsistent with prey stress models (PSMs). Predator-induced emigration during floods helped to maintain or increase predator impacts in flooded treatments. Nonlethal predator effects, and their potentially complex interaction with other biotic and abiotic factors during disturbance, may limit the success of ESMs. How disturbances modify predator impacts will depend on how direct and indirect predator effects interact with environmental factors to influence prey populations, not just on the relative tolerance of predators and prey to abiotic conditions.

ACKNOWLEDGMENTS

We thank Shane Brooks for use of the experimental stream channels, Maria Vazquez for field assistance and stimulating discussions on predation, and staff at the Cumberlands River Reserve for logistic support. Barbara Dworakowski from Theiss Environmental Services Pty. Ltd. provided discharge data. This paper was much improved following constructive comments by Bobbi Peckarsky, Steve Kohler, and an anonymous reviewer. This project was supported by an Australian Postgraduate Award scholarship and a Cooperative Research Centre for Freshwater Ecology postgraduate scholarship to J. R. Thomson.

LITERATURE CITED

Allan, J. D. 1982. Feeding habits and prey consumption of three setipalpian stoneflies (Plecoptera) in a mountain stream. Ecology **63**:26–34.

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman & Hall, London, UK.

Allan, J. D., and B. P. Feifarek. 1989. Distances travelled by drifting mayfly nymphs: factors influencing return to the substrate. Journal of the North American Benthological Society **8**:322–330.

Anderson, N. H. 1992. Influence of disturbance on insect communities in Pacific Northwest streams. Hydrobiologia **248**:79–92.

Anderson, N. H., and D. M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. Ecology **49**:198–320.

Bond, N. R., and B. J. Downes. 2000. Flow-mediated disturbance in streams: an experimental test of the role of rock movement in reducing macroinvertebrate population densities. Marine and Freshwater Research **51**:333–337.

Boulton, A. J., C. G. Peterson, N. B. Grimm, and S. G. Fisher. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrological disturbance regime. Ecology **73**:2192–2207.

Brittain, J. E., and T. J. Eikland. 1988. Invertebrate drift–a review. Hydrobiologia **166**:77–93.

Brooks, S. S. 1998. Impacts of flood disturbance on the macroinvertebrate assemblage of an upland stream. Dissertation. Monash University, Melbourne, Victoria, Australia.

Brooks, S. S., and A. J. Boulton. 1991. Recolonization dynamics of benthic macroinvertebrates after artificial and natural disturbances in an Australian temporary stream. Australian Journal of Marine and Freshwater Research **42**: 295–308.

Cerri, R. D., and D. F. Fraser. 1983. Predation and risk in foraging minnows: balancing conflicting demands. American Naturalist **121**:552–561.

Ciborowski, J. J. 1983. Downstream and lateral transport of nymphs of two mayfly species Ephemeroptera. Canadian Journal of Fisheries and Aquatic Sciences **40**:2025–2029.

Clements, W. H., D. S. Cherry, and J. Cairns, Jr. 1989. The influence of copper exposure on predator–prey interactions in aquatic insect communities. Freshwater Biology **21**:483–488.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 *in* M. L. Cody, and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Cooper, S. D., S. J. Walde, and B. L. Peckarsky. 1990. Prey exchange rates and the impact of predators on prey populations in streams. Ecology **71**:1503–1514.

Davis, J. A., and L. A. Barmuta. 1989. An ecologically useful classification of mean and near-bed flows in streams and rivers. Freshwater Biology **21**:271–282.

Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. Ecology **76**:1446–1460.

Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic biology and behaviour. Canadian Journal of Zoology **65**:803–811.

Downes, B. J., P. S. Lake, A. Glaister, and J. A. Webb. 1998. Scales and frequencies of disturbance: rock size, bed packing and variation among upland streams. Freshwater Biology **40**:625–639.

Elliot, L. M. 1971. The distances travelled by drifting invertebrates in a Lake District stream. Oecologia **6**:350–379.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. Ecology **78**:2316–2325.

Englund, G., and T. Olsson. 1996. Treatment effects in a stream fish enclosure experiment: influence of predation rate and prey movements. Oikos **77**:519–528.

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

Flecker, A. S., and B. Feifarek. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. Freshwater Biology **31**:131–142.

Glasby, T. M., and A. J. Underwood. 1996. Sampling to differentiate between pulse and press perturbations. Environmental Monitoring and Assessment **42**:241–252.

Hart, D. D., and R. A. Merz. 1998. Predator–prey interactions in a benthic stream community: a field test of flow-mediated refuges. Oecologia **114**:263–273.

Hildrew, A. G., and P. S. Giller. 1994. Patchiness, species interactions, and disturbance in the stream benthos. Pages 21–62 *in* P. S. Giller, A. G. Hildrew, and D. G. Raffaelli, editors. Aquatic ecology: scale, pattern and process. Blackwell Science, Oxford, UK.

Huberty, C. J., and J. D. Morris. 1989. Multivariate analysis versus multiple univariate analyses. Psychological Bulletin **105**:302–308.

Hynes, H. B. N., and M. E. Hynes. 1975. The life histories of many of the stoneflies [Plecoptera] of southeastern mainland Australia. Australian Journal Marine and Freshwater Research **26**:113–153.

Kerfoot, C. W., and A. Sih. 1987. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Kiesecker, J. 1996. pH-mediated predator–prey interactions between *Ambystoma tigrinum* and *Pseudacris triseriata*. Ecological Applications **6**:1325–1331.

Kiffney, P. M. 1996. Main and interactive effects of invertebrate density, predation, and metals on a Rocky Mountain stream macroinvertebrate community. Canadian Journal of Fisheries and Aquatic Sciences **53**:1595–1601.

Kratz, K. W. 1996. Effects of stoneflies on local prey populations: mechanisms of impact across prey density. Ecology **77**:1573–1585.

Lake, P. S. 1990. Disturbing hard and soft bottom communities: a comparison of marine and freshwater environments. Australian Journal of Ecology **15**:477–488.

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society **19**:573–592.

Lancaster, J. 1996. Scaling the effects of predation and disturbance in a patchy environment. Oecologia **107**:321–331.

Lancaster, J., and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. Journal of the North American Benthological Society **12**:385–393.

Lancaster, J., A. G. Hildrew, and C. Gjerlov. 1996. Invertebrate drift and longitudinal transport processes in streams. Canadian Journal of Fisheries and Aquatic Sciences **53**:572–582.

Lima, N. R., and L. M. Dill. 1990. Behavioural decisions made under risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619–640.

Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences **49**:617–628.

Malmqvist, B., and P. Sjörström. 1980. Prey size and feeding patterns in *Dinocras cephalotes* [Perlidae]. Oikos **35**:311–316.

Malmqvist, B., and P. Sjostrom. 1987. Stream drift as a consequence of disturbance by invertebrate predators: field and laboratory experiments. Oecologia **74**:396–403.

Marchant, R. 1988. Vertical distribution of benthic invertebrates in the bed of the Thomson River, Victoria. Australian Journal of Marine and Freshwater Research **39**:775–784.

Marchant, R. 1989. A subsampler for samples of benthic invertebrates. Bulletin of the Australian Society for Limnology **12**:49–52.

Matthaei, C. D., U. Uehlinger, E. I. Meyer, and A. Frutiger. 1996. Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. Freshwater Biology **35**:233–248.

Matthaei, C. D., D. Werthmüller, and A. Frutiger. 1997. Invertebrate recovery from a bed-moving spate: the role of drift versus movements inside or over the substratum. Archiv für Hydrobiologie **140**:221–235.

McLellan, I. D. 1996. A revision of *Stenoperla* [Plecoptera: Eusthiniidae] and removal of Australian species to *Cosmioperla* new genus. New Zealand Journal of Zoology **23**:165–182.

McPeek, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. Ecology **79**:867–879.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator–prey fish species. Ecology **65**:1525–1534.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs **46**:355–393.

Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology & Evolution **5**:52–57.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist **110**:351–369.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist **130**:730–757.

Miller, A. M., and S. W. Golladay. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial stream. Journal of the North American Benthological Society **15**:670–689.

Peckarsky, B. L. 1980. Predator–prey interactions between stoneflies and mayflies: behavioral interactions. Ecology **61**:932–943.

Peckarsky, B. L. 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pages 303–323 *in* T. D. Fontaine III and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor Michigan, USA.

Peckarsky, B. L. 1987. Mayfly cerci as defense against stonefly predation: deflection and detection. Oikos **48**:161–170.

Peckarsky B. L. 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. Ecology **77**: 1888–1905.

Peckarsky B. L., and C. A. Cowan. 1995. Microhabitat and activity periodicity of predatory stoneflies and their mayfly prey in a western Colorado stream. Oikos **74**:513–521.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology **74**:1836–1846.

Peckarsky, B. L., S. C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh–benign hypothesis. Freshwater Biology **24**:181–191.

Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia **113**:565–576.

Peckarsky, B. L., and M. A. Penton. 1989*a*. Mechanisms of prey selection by stream-dwelling stoneflies. Ecology **70**: 1203–1218.

Peckarsky, B. L., and M. A. Penton. 1989*b*. Early warning lowers risk of stonefly predation for a vulnerable mayfly. Oikos **54**:301–309.

Power, M. E. 1990. Effects of fish on river food webs. Science **25**:811–813.

Power, M. E., W. J. Matthews, and A. J. Sewart. 1985. Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. Ecology **66**:1448–1456.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7**:433–455.

Rykiel, E. J. 1985. Towards a definition of ecological disturbance. Australian Journal of Ecology **10**:361–365.

Sephton, D. H., and H. B. N. Hynes. 1983. Food and mouthpart morphology of the nymphs of several Australian Plecoptera. Australian Journal of Marine and Freshwater Research **34**:893–908.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution **13**:350–355.

Sih, A., and D. E. Wooster. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology **75**: 1199–1207.

Soluk, D. A., and J. S. Richardson. 1997. The role of stoneflies in enhancing growth of trout: a test of the importance of predator–predator facilitation within a stream community. Oikos **80**:214–219.

Thomson, J. R. 1999. Effects of disturbance on the impact of invertebrate predators in stream benthic communities. Dissertation. Monash University, Melbourne, Victoria, Australia.

Townsend, C. R., and A. G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology **31**:265–275.

Townsend, C. R., M. R. Scarsbrook, and S. Doledec. 1997. Quantifying disturbance in streams: alternative measures of disturbances in relation to macroinvertebrate species traits and species richness. Journal of the North American Benthological Society **16**:531–44.

Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities. Pages 151–180 *in* D. R. Strong, D. Simberloff, L. Abele, and A. Thistle, editors. Ecological communities: conceptual issues and evidence. Princeton University Press, Princeton, New Jersey, USA.

Vazquez, M. 1998. Interactions between insect predators in a rocky stream in south-eastern Australia. Dissertation. Monash University, Melbourne, Victoria, Australia.

Walde, S. J. 1986. Effect of an abiotic disturbance on a lotic predator–prey interaction. Oecologia **69**:243–247.

Wallace J. B., T. F. Cuffney, C. C. Lay, and D. Vogel. 1987. The influence of an ecosystem level manipulation on prey consumption by a lotic dragonfly. Canadian Journal of Zoology **65**:35–40.

Walton, O. E., Jr. 1980. Invertebrate drift from predator–prey associations. Ecology **61**:1486–1497.

Williams, D. D. 1987. A laboratory study of predator–prey interactions of stoneflies and mayflies. Freshwater Biology **17**:471–490.