Ecology, 85(8), 2004, pp. 2279–2290
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PREDATOR-INDUCED RESOURCE HETEROGENEITY IN A STREAM FOOD WEB

ANGUS R. MCINTOSH,[1,2,5] BARBARA L. PECKARSKY,[1,3] AND BRAD W. TAYLOR[1,4]

[1]*Rocky Mountain Biological Laboratory, P.O. Box 529 Crested Butte, Colorado 81224 USA*
[2]*School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand*
[3]*Department of Entomology, Cornell University, Ithaca, New York 14853 USA*
[4]*Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*

Abstract. Heterogeneous distributions of resources and organisms are characteristic of most ecosystems, but empirical understanding of the causes and consequences of heterogeneity is limited. We investigated whether predatory fish influenced the heterogeneity (spatial variability) of resources (algae) by modifying the behavior of primary consumers (mayflies). We hypothesized that fish would indirectly increase resource heterogeneity by reducing grazer activity, and that higher densities of grazers would reduce resource heterogeneity only in the absence of fish. We measured the effects of predator cues (brook trout odor) on grazer behavior (*Baetis*) and algal heterogeneity in mesocosms (~1 m^2) and in simple natural systems (30-m reaches of adjacent fishless streams). In addition, we measured grazer and algal distributions in complex natural streams that varied in grazer density, presence of fish, and physical conditions. Fish odor altered mayfly grazing behavior (measured using a simple behavioral bioassay) and increased algal heterogeneity (measured by Morisita's index at the scale of individual rocks) in mesocosms and manipulated streams. Furthermore, natural streams with higher grazer densities had lower algal heterogeneity, but only if they were fishless. Interestingly, the presence of brook trout decoupled the link between grazer density and algal heterogeneity in natural streams. These observations indicate that release from the threat of predation or increased densities of grazers can homogenize algal resources in fishless streams. We hypothesize that altered foraging in environments with predatory fish, independent of grazer density, led to increased resource patchiness, possibly by allowing the influence of variation in physical characteristics (e.g., flow and substratum) to predominate or by changing grazer microhabitat use. These results support theoretical predictions that factors affecting primary consumer behavior also alter resource heterogeneity.

Key words: algae; grazers; mayflies; Morisita index; predator–prey interactions; resource heterogeneity; streams; trout chemical cues.

INTRODUCTION

The world is heterogeneous, and this has far-reaching ecological implications (Stewart et al. 2000). Although heterogeneity comes in many different forms (Kolasa and Rollo 1991, Wiens 2000), we use the term here in its simplest form to refer to spatial variability resulting in distribution patterns that are patchy or aggregated (Ettema and Wardle 2002). Theory suggests that spatial heterogeneity of habitats and organisms can alter the richness, abundance fluctuations, and organization of communities (Kareiva 1990, Hassell et al. 1994, Tilman 1994). For example, populations may be more persistent in patchy habitats (Ellner et al. 2001), and heterogeneity in spatial distributions created by biological interactions may enhance diversity (Sommer 2000). Despite the importance of heterogeneity in ecological communities, we have limited empirical understanding of its causes and consequences (Steinberg and Kareiva 1997, Wiens 2000). Addressing this problem requires consideration of heterogeneity in organism abundance as a more relevant response variable than mean abundance (Palmer et al. 1997).

Heterogeneity in habitats, and resource and consumer distributions, may be mediated by physical conditions (Wiens 2000), or generated by organisms (Pickett et al. 2000). For example, the spatial pattern of soil nutrient levels is affected by topography and precipitation (Burke et al. 1997, Ettema and Wardle 2002), and further modified by herbivores, which remove vegetation and excrete nutrients (Frank and Groffman 1998, Augustine and Frank 2001). Similarly, patchy distributions of stream organisms may be caused by spatial variation in flow (Hart and Finelli 1999) and by interactions with other organisms (Hildrew and Giller 1994). Furthermore, consumers also respond to changes in patch quality and interact with competitors and predators, often resulting in complex interactions between consumers and resource patchiness (Brown 2000). For example, by influencing the distribution, abundance, and movement of consumers (Lima 1998),

Manuscript received 24 March 2003; revised 16 October 2003; accepted 19 December 2003. Corresponding Editor: B. Downes.
[5] E-mail: angus.mcintosh@canterbury.ac.nz

predators could affect indirectly the heterogeneity of consumer resources (Abrams 2000).

In this study, we investigated whether predators (trout) in streams could influence the heterogeneity of resources (algae) by modifying the behavior of primary consumers (mayflies) in environments that were themselves heterogeneous (e.g., variability in current velocity). Streams have long been recognized as heterogeneous systems (Hynes 1970, Hildrew and Giller 1994); but stream ecologists have only recently begun to characterize that heterogeneity and determine its causes and consequences (e.g., Downes et al. 1993, Cooper et al. 1997, Crowl et al. 1997, Palmer et al. 1997). Algal resources in streams are patchy at many scales (Stevenson 1983), and while moving among algal patches consumers affect not only the abundance (Lamberti and Moore 1984), but also the heterogeneity of their resources (Lamberti and Resh 1983, Sarnelle et al. 1993). Depending on whether predators restrict or stimulate movement of grazing prey, different patterns of algal heterogeneity would be predicted in predator and predator-free habitats (Abrams 2000).

Predators can alter the periodicity and amount of prey movement in streams (e.g., Cooper et al. 1990, Sih and Wooster 1994). For example, visually feeding trout present a higher predation risk during the day than night (e.g., Allan 1981, McIntosh et al. 2002), resulting in reduced daytime drift of mayflies in the water column, and changes in nocturnal drift (e.g., Douglas et al. 1994, McIntosh et al. 2002). Avoidance of predation may also reduce mayfly foraging time by restricting grazers to nocturnal use of algae-covered upper surfaces of rocks (Cowan and Peckarsky 1994, McIntosh and Townsend 1995). Such predator-induced changes in consumer foraging may cause different patterns of resource heterogeneity in streams with and without trout.

Tests of predictions from conceptual models

We tested two hypotheses based on the assumption that unconstrained movement of grazing mayflies homogenizes algal distributions. Two-patch models (Abrams 2000) predicted that predators could affect resource heterogeneity by interfering with patch selection and movement of their prey. These models consistently predicted that maximum resource heterogeneity would be observed at intermediate rates of consumer movement. In particular, resource heterogeneity should increase when consumer movement is reduced if the grazing rate of unconstrained consumers is faster than resource growth rate. Thus, predators should increase heterogeneity of algal resources by reducing movements of relatively mobile foragers like mayflies (hypothesis 1). Therefore, we expected to observe higher natural heterogeneity of algae in streams containing fish than in fishless streams.

Second, we hypothesized that predators could decouple the relationship between algal heterogeneity and grazer density by altering grazing behavior. In Venezuelan piedmont streams, Flecker and Taylor (*unpublished manuscript*) observed maximum resource heterogeneity of organic sediments and biofilms at intermediate densities of grazing fish, because very low densities were insufficient to generate resource patchiness and very high consumer densities uniformly reduced resources. However, we expected that such relationships between grazer densities and algal heterogeneity might only be observed in the absence of fish where grazer behavior was unconstrained (hypothesis 2).

Recognizing that variation in physical conditions influences the distribution of resources, consumers and predators (Hart and Finelli 1999), and the outcome of their interactions, we tested our hypotheses in three different studies that varied in habitat heterogeneity. First, we determined whether simulated predation risk (fish odor) could generate resource heterogeneity in mesocosms ($\sim$1 m^2, the ''mesocosm experiment''), where we could control variation in habitat heterogeneity and mayfly abundance, and more easily observe grazer behavior. Second, we added fish odor to 30-m long reaches of similar, adjacent, fishless streams (the ''whole-stream manipulation''), and measured whether predators caused changes in grazer behavior and resource heterogeneity in relatively simple natural systems. Finally, we observed grazer and algal distributions in streams that varied in grazer density, presence of fish, and physical conditions to determine whether we could observe similar patterns against the backdrop of natural complexity.

METHODS

We measured algal heterogeneity at the scale of individual rocks, because many mayfly grazers move among rocks by drifting to locate high quality food patches (Kohler 1984, Peckarsky 1996). We used the Morisita index of aggregation (Krebs 1999) to assess the spatial heterogeneity of algae and grazers on rocks:

$$I_d = n\left[\frac{\sum x^2 - \sum x}{\left(\sum x\right)^2 - \sum x}\right] \quad (1)$$

where I_d = Morisita's index; n = number of samples; and x = abundance in a sample. This index is one of the most robust for characterizing spatial variability (Krebs 1999). Although there can be systematic bias at low population densities (Downing 1991), it is relatively independent of sample population density, and is preferable to traditional measures of spatial distribution, such as the variance:mean ratio (Hurlbert 1990).

Artificial stream experiment (mesocosms)

As in previous experiments (e.g., McIntosh and Peckarsky 1999) we added chemical cues from brook trout (*Salvelinus fontinalis*) to mesocosms stocked with

periphyton-covered rocks and natural densities of mayfly larvae (*Baetis bicaudatus* Dodds) to simulate a predation threat, while preventing prey consumption by predators. This method enabled us to unequivocally attribute changes in grazer or algal spatial distribution to predator-induced alterations in grazer behavior.

Circular flow-through mesocosms (wetted surface area, 0.82 m^2; mean water depth, 21 cm) were constructed from gray plastic cattle watering tanks (see Fig. 1 in Peckarsky and McIntosh 1998), and located adjacent to the East River at the Rocky Mountain Biological Laboratory (RMBL) in western Colorado. Filtered water was gravity fed from a small fishless stream, and water temperature ranged 4–10°C daily. We created four resource ''patches'' in the mesocosms each with four diatom-covered rocks (mean width, 15 cm) from the East River. Physical heterogeneity within the mesocosms was controlled by variation in current velocity, which enabled two patches of cobbles to be placed in faster (35.7 ± 1.1 cm/s [mean ± 1 SE]) and two in slower current (9.8 ± 0.3 cm/s). Current velocity was measured at 0.6 m water depth above cobbles with a Marsh-McBirney Flo-Mate meter (Frederick, Maryland, USA).

On 7 July 1998, we added 300 *Baetis* from a fishless tributary of the East River to 10 mesocosms, simulating natural densities (365 individuals/m^2, Peckarsky et al. 2001). We used late-instar larvae without black wingpads (head capsule width: males = 0.99 ± 0.03 mm, $N = 16$; females = 0.92 ± 0.01 mm, $N = 34$ [mean ± 1 SE]). The mean (± 1 SE) number of *Baetis* remaining at the end of the experiment was 296 ± 2 (range: 284–300, $N = 10$). Since we controlled grazer density, this experiment was designed to test only the first hypothesis (effects of predators on algal heterogeneity).

Two brook trout (151 and 234 mm fork length [FL]) were added to a 110-L holding tank that received the same fishless water as the mesocosms. Brook trout were fed a mixed diet of stream invertebrates every other day. Water from the fish-holding tank was delivered to half of the mesocosms through spouts (mean = 1.17 L/min), and the other half received fishless water at a similar rate ($N = 5$). We also added predatory stoneflies (two males and six females of *Megarcys signata*, Plecoptera: Perlodidae; head capsule widths: males = 3.32 ± 0.06 mm; females = 4.35 ± 0.09 mm [mean ± 1 SE]) to each mesocosm, because predatory stoneflies occur in all streams of this study (Peckarsky et al. 2001), and affect responses of mayflies to fish (Peckarsky and McIntosh 1998). We glued the mouthparts of stoneflies with barge cement to prevent feeding, but allow natural foraging (Peckarsky and McIntosh 1998). The stonefly density used was representative of those in the natural habitat (Peckarsky 1991).

For the first 3 days of the experiment, we observed the number of mayflies grazing on exposed rock surfaces and the number drifting past a transect in each mesocosm for 2 min at 1000 hours and 2200 hours (mountain daylight saving time). At night, we used dim red light from headlamps covered with red filters (Peckarsky and McIntosh 1998).

After 9 days, we randomly selected eight rocks from each mesocosm (2 from each ''patch'') for analysis of algal biomass. We used a toothbrush to remove periphyton from the upper surface of each rock, filtered the periphyton onto glass fiber filters (Whatman GF/C), extracted pigments for 24 h in 90% ethanol, then analyzed for chlorophyll *a* using a spectrophotometer (Nusch 1980). The upper surface area of each rock was determined by wrapping it in aluminum foil, the weight of which was used to extrapolate upper surface area from a standard curve.

We used repeated-measures ANOVA with a split-plot design to test the effects of fish odor and current velocity (fixed variables) on a simple behavioral bioassay of grazing activity (the number of *Baetis* visible on stones) during the day and night using mesocosms as replicates for the odor effect. Data were $\ln(x + 1)$ transformed to meet the assumptions of ANOVA. We tested the effect of fish odor on the heterogeneity of *Baetis* distributions (Morisita's index, I_d, calculated from counts of *Baetis* visible on 16 rocks in each mesocosm) during day and night with time of day as the repeated measure.

We also simultaneously ran two control treatments in six mesocosms with similar algal covered rocks arranged in fast and slow patches, but with no grazers; half these control mesocosms received fish odor and half fishless water ($N = 3$). These treatments enabled us to determine whether fertilization from the fish tank affected algal biomass, and to compare algal biomass and heterogeneity with and without grazers. First, we tested the effects of grazers and fish odor on the mean abundance of algae using two-way ANOVA with unequal replication. Second, split-plot ANOVAs (as described in the last paragraph) were run separately on treatments with and without grazers to assess the influence of fish odor and current velocity on algal abundance. Finally, a one-way ANOVA with an a priori contrast tested if the presence of grazers affected the Morisita algae index.

Whole-stream manipulation

During July 1999, we placed 110 L plastic bins near the headwaters of 10 naturally fishless tributaries of the East River at RMBL (Tables 1 and 2; also see Peckarsky et al. 2002 for more details). Intake and outflow hoses gravity-fed fishless water from upstream through the bins and then back into the stream (2.5–3.0 L/min). We placed two brook trout (mean FL ± 1 SE = 155 ± 6 mm) in bins alongside five randomly allocated streams, the other five streams acting as controls. Brook trout were fed a mixed diet of stream invertebrates every other day. This protocol enabled us to measure the effect of fish chemical cues on the for-

TABLE 1. The physicochemical characteristics of the streams used in (a) the whole-stream manipulation experiment and (b) the field survey of natural streams in 1997 (for details of measurement methods for [a] and [b], see Peckarsky et al. [2002] and McIntosh et al. [2002], respectively).

Experiment and treatment	Mean temperature (°C)	Channel width (m)	Mean depth (cm)	Mean current velocity (cm/s[1])
a) Whole-stream experiment‡				
Control streams	6.0 (0.5)	0.53 (0.05)	6.0 (0.8)	38 (5)
Fish odor streams	6.3 (0.7)	0.47 (0.05)	5.1 (0.6)	34 (3)
b) Natural streams§				
Fishless streams	8.0 (5.7–12.6)	2.0 (0.8–5.0)	7.4 (4–14)	41 (20–68)
Trout streams	7.8 (6.1–10.2)	6.1 (1.4–10.5)	18 (9–22)	53 (22–73)

Notes: Standard errors for means are given in parentheses for the whole-stream experiment, and ranges are given in parentheses for natural streams. Ellipses (⋯) indicate that no brook trout were present in the experimental streams.

† Substratum particle size was measured by a size index in the whole-stream experiment (see Peckarsky et al. 2002) and by median particle size in the natural streams (cm).

‡ Values are from Peckarsky et al. (2002), with predatory invertebrate densities reported in that paper corrected for an error in sampler size.

§ Values are from McIntosh et al. (2002).

aging behavior of grazers and algal heterogeneity (hypothesis 1); and whether predators affected the relationship between grazer density and algal heterogeneity (hypothesis 2) under natural conditions in small, relatively simple streams.

We estimated the natural variation in densities of grazers among streams by taking three Hess samples (0.09 m^2) along 30 m reaches of each stream before and 3 wk after the odor addition (29 July and 20 August). We also recorded the numbers of grazers (mayflies and caddisflies) visible on the substratum surface at 15 randomly selected locations in each stream using a glass-bottom viewing box (0.04 m^2). Observations were made at 1000 hours and 2200 hours (using dim red light) before (27 July) and after (2 August) the addition of fish odor. We used repeated-measures ANOVA (before vs. after odor addition) to determine whether grazer densities were affected by trout odor. To test whether daytime use of substratum surfaces by mayflies and caddisflies (a simple bioassay of grazing behavior) was affected by trout odor addition we used Mann-Whitney *U* tests on the net change in the number of grazers observed before compared to after the addition (where net change = ln[after + 1]−ln[before + 1]). This nonparametric test was used because observations of zero grazers rendered transformations ineffective in satisfying assumptions of parametric statistics.

To estimate algal biomass and heterogeneity, we randomly selected 15 representative rocks (mean width: 6.5 cm) from the 30 m reaches in each stream and extracted whole rocks in 90% ETOH for chlorophyll *a* analysis. We calculated Morisita's index using chlorophyll *a* from 15 rocks in each stream, and used a *t* test to determine whether fish odor affected resource heterogeneity (hypothesis 1). To test hypothesis 2, we used a homogeneity-of-slopes test to assess the effect of grazer density (mayflies and caddisflies in Hess samples) on Morisita's index of algal patchiness in fish odor and control streams (odor treatment × grazer density interaction). This test was followed by regressions to test whether the slopes of the relationships between grazer densities and algal heterogeneity in fish and fishless streams were significantly different.

Field survey

During late July, we estimated the abundance of predatory fish and invertebrate grazers in 30-m reaches in 10 (1997) and eight (1998) streams in the Upper East River catchment north of RMBL (Tables 1 and 2; see also Fig. 1 in Peckarsky et al. 2000 and Table 1 in McIntosh et al. 2002 for more information on the streams). Half the reaches were fishless, and the other half contained only brook trout, whose densities were obtained by three-pass electrofishing (see McIntosh et al. 2002 for details). The eight streams sampled in 1998 were a subset of those sampled in 1997, except for one fishless stream that was sampled for the first time in 1998. Invertebrate grazer densities were estimated from four area-delineated electrobug samples (0.092 m^2) taken at random locations within each reach (Taylor et al. 2001). We estimated algal biomass (chl *a*/cm^2) on 10 rocks randomly selected from each reach (1997), or from 10 rocks at relatively high-flow locations (mean ± 1 SE = 74.7 ± 1.3 cm/s) and 10 at low-flow (15.4 ± 1.3 cm/s) locations (1998). We removed periphyton from 7.06 cm^2 of the top of each rock with a toothbrush, and estimated chlorophyll *a* as above. We calculated Morisita's index using the chl *a* values for all rocks collected within each stream.

To compare the natural heterogeneity of algal resources between fish and fishless streams (hypothesis 1), we used two-factor ANOVA (year × presence of fish), which enabled us to determine whether fish effects depended on year. To assess the effects of fish predators on the relationship between grazer density and algal heterogeneity (hypothesis 2), we used a homogeneity-of-slopes test followed by individual linear

TABLE 1. Extended.

Discharge (1×10^{-2} m^3/s)	Conductivity (μS/cm at 25°C)	Substratum particle size†	Predatory invertebrates (no./m^2)	Brook trout biomass (g/m^2)
1.2 (0.2)	136 (8)	4.7 (0.1)	62 (28)	⋯
0.9 (0.2)	124 (5)	4.7 (0.1)	17 (4)	⋯
1.7 (0.2–3.8)	149 (126–187)	10 (6–18)	31.8 (7.4–72)	0
56 (3.7–122)	198 (181–270)	12 (7–17)	19.2 (7.4–46)	3.5 (0.7–14)

regressions on fish and fishless streams. These tests determined whether the slopes of the relationship between grazer density measured from benthic samples and Morisita index of algal heterogeneity differed between fish and fishless streams.

RESULTS

Mesocosm experiment

Grazer distributions and movement (behavioral bioassays).—As observed in previous experiments (e.g., McIntosh and Peckarsky 1999), *Baetis* drift was negligible during the day in mesocosms with trout odor, whereas daytime drift was observed in fishless mesocosms (Table 2). Fewer *Baetis* grazed on the tops of rocks during the day in fish odor than fishless mesocosms (Fig. 1a); whereas nighttime grazing was similar in fish odor and fishless mesocosms (Fig. 1a: significant time × odor interaction; Table 3a). Furthermore, a significant three-way interaction in the ANOVA (Table 3a) indicated that grazer use of microhabitat depended on both the time of day and fish odor. During the day mayflies in fish odor treatments avoided slow rocks, whereas mayflies in fishless treatments used fast and slow rocks similarly (Fig. 1a). During the night more

TABLE 2. The abundance and behavior of grazers and the abundance of algal resources (means [± 1 SE]) in streams with and without odor from predatory brook trout in a mesocosm experiment, a whole-stream manipulation experiment, and a survey of fish and fishless streams.

Experiment or observation	Grazer density (no./m^2)			Grazer movement (no. *Baetis* drifitng/2 min.)	Mean chl a (μg/50 cm^2)
	Baetis	Heptageniidae	Caddisflies		
Mesocosm experiment					
No grazers	⋯	⋯	⋯	⋯	46.7 (2.0)‖ 51.3/42.2#
Fishless	365	⋯	⋯	1.67 (0.34)	19.0 (2.0)‖ 18.7/19.3#
Fish	365	⋯	⋯	0	15.2 (1.0)‖ 14.2/16.0#
Whole-stream manipulation†					
Fishless	100 (34)	274 (32)	186 (96)¶	NM	141 (34)
Fish	69 (48)	179 (45)	194 (73)¶	NM	115 (15)
Natural streams					
Fishless	316 (168)‡ 380 (194)§	84 (31)‡ 447 (187)§	⋯	NM	62.5 (15.1)‡ 22.7 (10.3)§
Fish	296 (110)‡ 1021 (611)§	379 (120)‡ 756 (109)§	⋯	NM	29.0 (4.7)‡ 8.6 (1.3)§

Notes: Grazer densities were obtained from benthic electrobug samples (measured at the start, for experiments). Ellipses (⋯) indicate the taxon was not present, NM indicates variable was not measured.

† Invertebrate densities from Peckarsky et al. (2002) corrected for an error in the sampler size.

‡ July 1997.

§ July 1998.

¶ Caddisflies (*Neothremma* and *Allomyia* sp.) were common in the small streams used for the manipulation but were absent or very rare in other streams in the East River valley used for the comparison of natural fish and fishless streams.

‖ Mean (with 1 SE in parentheses) values from mesocosms.

Mean values from fast and slow rocks, respectively, in mesocosms.

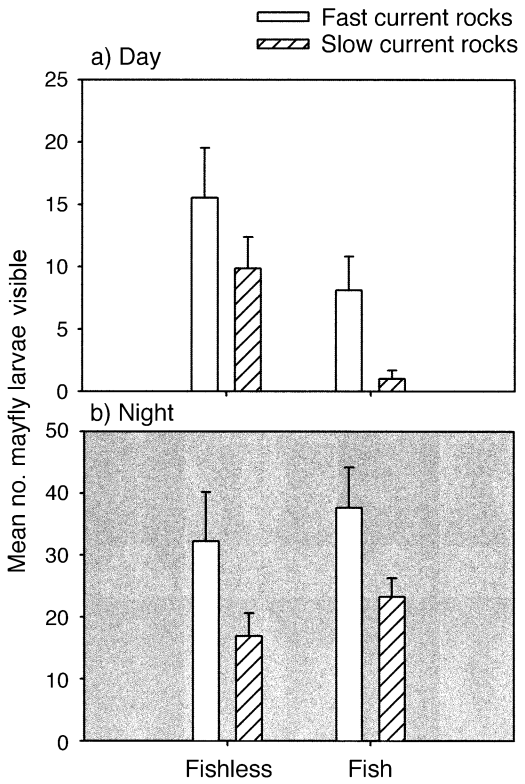


FIG. 1. Mean (+1 SE) number of *Baetis* mayfly larvae visible on tops of rocks in fast- and slow-current-velocity locations in the mesocosm experiment during (a) day and (b) night. Means and standard error bars were calculated using the average for fast or slow rocks from a mesocosm as replicates.

mayflies used fast rocks independent of fish odor (Fig. 1b). Morisita's index indicated that *Baetis* distributions on rocks in the mesocosms were always more heterogeneous in the day, independent of fish odor (Table 3b, Fig. 2).

Resource distribution.—Although mean chlorophyll *a* was higher in treatments without than with grazers (Table 2; ANOVA, grazer effect, $F_{1,12} = 181.0$, $P < 0.001$), predator odor did not affect the mean biomass of algae directly (nutrient enrichment in the absence of grazers) or indirectly (via effects on grazer behavior) (Table 2; ANOVA, odor effect, $F_{1,12} = 0.31$, $P = 0.59$; interaction, $F_{1,12} = 1.34$, $P = 0.27$). Furthermore, mean algal abundance did not differ between rocks in fast and slow currents in treatments with or without grazers, and there were no significant interactions between fish odor and current velocity (Table 4).

However, the presence of fish odor did affect the heterogeneity of algae in mesocosms (Fig. 3a). As predicted by hypothesis 1, Morisita's index for chlorophyll *a* in treatments with *Baetis* grazers was significantly higher in fish than in fishless treatments. Furthermore, both grazer treatments reduced resource heterogeneity compared to controls with no grazers (Fig. 3a).

Whole-stream manipulation

Grazer abundance.—The density of mayfly grazers in control and odor-addition streams did not differ before or after the addition of odor (Table 2; repeated-measures ANOVA; odor effect; $F_{1,8} = 0.784$, $P = 0.40$; time effect, $F_{1,8} = 1.498$, $P = 0.26$; time × odor interaction, $F_{1,8} = 0.004$, $P = 0.95$). Cased caddisflies (*Neothremma* and *Allomyia* sp.) were present in the streams at the start of the experiment, but numbers diminished significantly during the experiment due to pupation and emergence (Table 2; repeated-measures ANOVA; odor effect, $F_{1,8} = 0.0049$, $P = 0.95$; time effect, $F_{1,8} = 7.087$, $P = 0.029$; time × odor interaction, $F_{1,8} = 0.0038$, $P = 0.95$).

Grazer behavior (behavioral bioassay).—Addition of fish odor decreased the daytime use of exposed rock surfaces by *Baetis* and heptageniid mayflies (*Cinygmula* spp.) (Fig. 4; $U = 22$, $P = 0.045$), although night use was unaffected ($U = 9.5$, $P = 0.53$). In contrast, use of exposed rock surfaces by grazing caddisflies was unaffected by fish odor ($U = 15$, $P = 0.60$ and $U = 18$, $P = 0.25$ for day and night, respectively).

Resource distribution.—Algal standing crop (mean chlorophyll *a*) did not differ between the fish odor and control streams after the odor addition (Table 2; $t = 0.70$, df = 8, $P = 0.50$). However, as in the mesocosm experiment, and as predicted by hypothesis 1, the patchiness of algal resources was significantly higher in streams receiving fish odor (Fig. 3b). (Note: we excluded one outlier stream from the analysis because of a radically different temperature regime that could affect algal resources [maximum temperatures 9°C greater than average of other streams and mean temperature 3°C greater than average of other streams].) Overall, resource heterogeneity was lower in the controlled environments (mesocosms) than in natural streams (Fig. 3a vs. b). With regard to hypothesis 2, we found no linear effects of grazer density on heterogeneity of chlorophyll *a* in either odor or control streams (Fig. 5a).

Alternative explanations.—Fish odor and control streams did not differ with respect to cumulative degree days over 0°C, substratum particle size, water depth, stream width, current velocity, discharge, conductivity, densities of predatory stoneflies or grazers (Tables 1 and 2, also see Table 1 in Peckarsky et al. 2002). Thus, we could not attribute observed differences in grazer behavior and algal distribution between the two types of streams to any measured abiotic or biotic factors other than the presence of fish odor. Finally, since mean algal densities did not differ among treatments, results of this experiment could not be explained by systematic bias whereby higher values of Morisita's index (I_d) occur at lower population densities (Downing 1991).

Natural streams

In natural streams dominated by *Baetis* and other grazing mayflies (caddisfly grazers were negligible: Ta-

TABLE 3. Results of repeated-measures ANOVA testing the effects of fish odor, current velocity, and time of day (repeated measure) on the $\log_e$-transformed (a) number of *Baetis* mayflies visible on the tops of rocks and (b) heterogeneity of *Baetis* distributions measured by Morisita's index (I_d).

Source	df	MS	F	P
a) Number of grazers visible				
Between subjects				
Odor	1	2.272	25.02	<0.01
Mesocosms(odor)	8	0.091		
Current	1	5.683	28.73	<0.001
Odor × current	1	0.628	3.174	0.11
Error	8	0.199		
Within subjects				
Time	1	18.07	225.3	<0.001
Time × odor	1	4.812	28.51	<0.001
Time × mesocosm(odor)	8	0.169		
Time × current	1	0.448	5.590	0.0457
Time × odor × current	1	1.151	14.34	<0.01
Error	8	0.080		
b) Grazer I_d				
Between subjects				
Odor	1	1.676	1.702	0.23
Error	8	0.985		
Within subjects				
Time	1	11.66	12.86	<0.01
Time × odor	1	1.485	1.648	0.24
Error	8	0.907		

Note: For panel (a) we used a split-plot design to assess the effect of current velocity and fish odor, with mesocosms (a random factor) as replicates for the fish odor effect.

ble 2), mean algal biomass (chlorophyll *a*) was significantly higher in fishless than fish streams in both 1997 and 1998, and mean algal biomass was higher in 1997 than 1998 (Table 2; two-factor ANOVA; fish-treatment effect, $F_{1,14} = 7.43$, $P = 0.016$; year effect, $F_{1,14} = 19.6$, $P < 0.001$). Contrary to hypothesis 1, the heterogeneity of algal resources did not differ between fish and fishless streams in either year (Fig. 3c). However, in both years algal heterogeneity decreased significantly with increasing grazer density, but only in fishless streams (Fig. 5b and c).

A power analysis (Zar 1984) estimated that in both years the power was >0.75 to detect a difference in algal heterogeneity (I_d) between fish and fishless streams similar in magnitude to that observed in the whole stream experiment. Thus, the lack of significant differences in mean algal heterogeneity in natural fish and fishless streams was unlikely to be due to a lack of statistical power. Furthermore, despite low statistical power (caused by small sample sizes) to detect a sig-

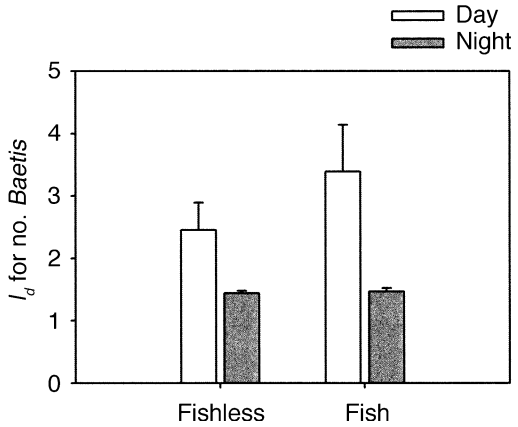


FIG. 2. Mean (+1 SE) Morisita's index (I_d) of heterogeneity for the number of *Baetis* larvae on tops of rocks during day and night in mesocosms with and without fish odor. Means and standard errors were calculated using mesocosms as replicates.

TABLE 4. Results of split-plot ANOVA testing the effects of current velocity and fish odor in the mesocosm experiment on the abundance of algae ($\log_e$-transformed chlorophyll *a*) from (a) mesocosms with grazers and (b) mesocosms without grazers.

Source	df	MS	F	P
a) Mesocosms with grazers				
Odor	1	0.212	1.454	0.26
Mesocosms(odor)	8	0.146		
Current	1	0.0429	1.866	0.21
Odor × current	1	0.0062	3.174	0.62
Error	8	0.0230		
b) Mesocosms without grazers				
Odor	1	0.0002	0.0042	0.95
Mesocosms(odor)	8	0.0481		
Current	1	0.1511	0.796	0.42
Odor × current	1	0.0017	0.009	0.93
Error	8	0.1899		

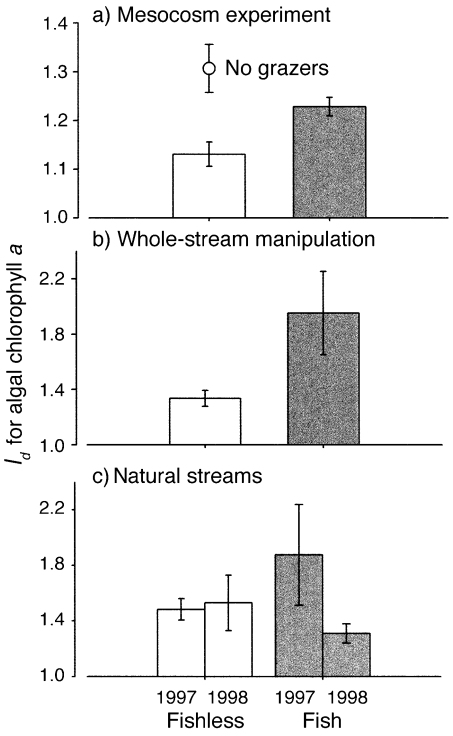


FIG. 3. Mean (±1 SE) Morisita's index (I_d) of heterogeneity for algal chlorophyll *a* with (gray bars) and without (white bars) brook trout odor. (a) Mesocosms with *Baetis* (eight rocks sampled): Morisita's index, fish odor > fishless (t = 3.09, df = 8, P = 0.014); Morisita's index, no grazers > grazers (single-factor ANOVA, contrast, $F_{1,12}$ = 18.93, P < 0.001); the mean for treatments with no grazers (labeled open circle) was calculated using all mesocosms without grazers as replicates. (b) Whole-stream manipulation (15 rocks): Morisita's index for chlorophyll *a*, fish odor > fishless (t = 3.07, df = 7, P = 0.018 after removal of outlier; t = 2.01, df = 8, P = 0.079 with all streams included). (c) Natural streams in July 1997 (10 rocks from each of five fish and five fishless streams) and July 1998 (20 rocks from each of four fish and four fishless): Morisita's index for chlorophyll *a* did not differ between fish and fishless streams in either year (fish treatment effect, $F_{1,14}$ = 0.358, P = 0.55; year effect, $F_{1,14}$ = 0.71, P = 0.41; interaction: $F_{1,14}$ = 1.48, P = 0.24). Note the different axis scales indicating that overall resource heterogeneity was lower in the controlled environments (mesocosms). In all cases, means and standard errors were calculated using mesocosms or streams as replicates.

nificant correlation between grazer density and algal heterogeneity (<0.6 in all cases), we still observed a significant relationship in fishless streams in both years. Moreover, bias in I_d associated with different algal densities could not explain the different relationships between grazer density and I_d observed in natural streams with and without fish.

DISCUSSION

Heterogeneous distributions of resources and consumers are characteristic of many ecosystems (Wiens 2000, Adler et al. 2001, Ettema and Wardle 2002). If predators alter the behavior and patch selection of their prey (Lima 1998), there is potential for behavioral interactions between predators and prey to affect both the heterogeneity of prey and distributions of resources. Our data demonstrate that primary consumers can alter the heterogeneity of their resources and that predators by affecting the behavior of primary consumers can indirectly influence resource heterogeneity.

We observed increased heterogeneity of algae in the presence of a predation threat from brook trout in mesocosms and experimental streams, and the presence of brook trout decoupled the link between grazer density and algal heterogeneity in natural streams. These observations support the predictions of both hypotheses: (1) grazers decreased the patchiness of algae at the scale of individual rocks when released from the threat of predation, and (2) increasing densities of unconstrained grazers also reduced resource heterogeneity.

In both experiments, trout consumption of mayflies was excluded and mayfly densities were not significantly different between fishless and fish-odor treatments. Thus, these experiments provide strong evidence that predator-induced changes in grazer behavior were responsible for the observed changes in resource heterogeneity. *Baetis* mayflies strongly select high

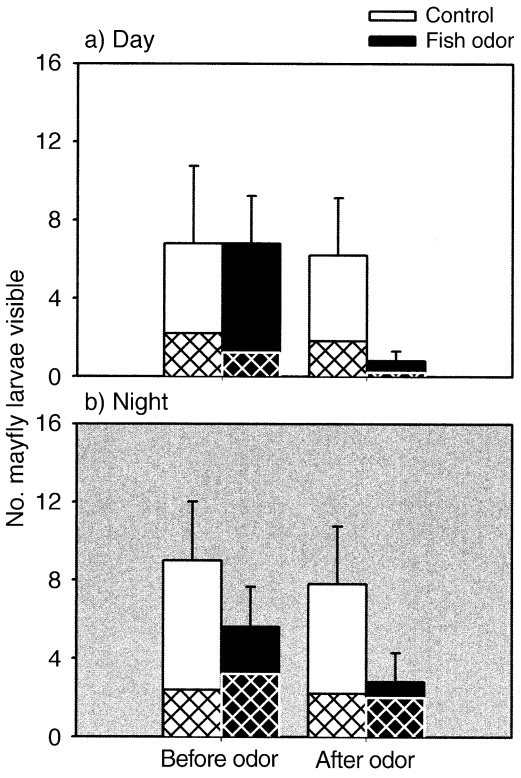


FIG. 4. Mean (+1 SE) total number of mayfly larvae observed on the upper surfaces of 15 substrates per stream during the (a) day and (b) night in five odor-treated and five control streams before and after the addition of brook trout odor. Open and hatched bars indicate numbers of *Baetis* and heptageniid (*Cinygmula*) larvae, respectively. Means and error bars were calculated using streams as replicates.

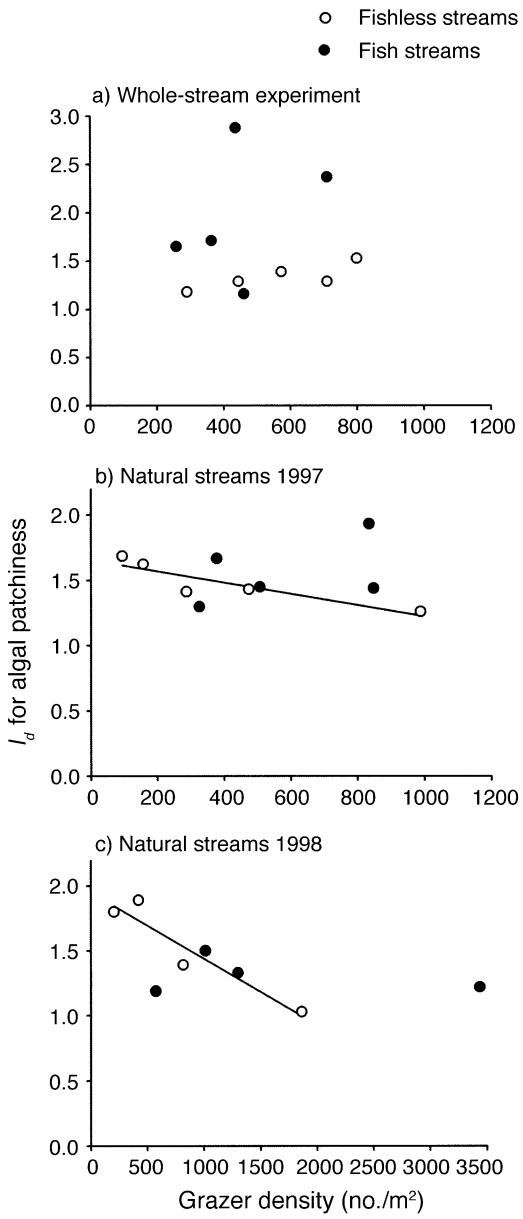


FIG. 5. Morisita's index (I_d) for algal patchiness based on chlorophyll *a* from individual rocks plotted against the density of total grazers: (a) 15 rocks from five control streams and five streams receiving fish odor in the 1999 whole-stream manipulation, (b) natural streams in 1997 (10 rocks), and (c) 1998 (20 rocks). The homogeneity-of-slopes test for the whole-stream manipulation showed in (a) no odor treatment × grazer density interaction ($F_{1,6} = 0.232$, $P = 0.65$) and no grazer density effect (ANCOVA, $F_{1,7} = 0.233$, $P = 0.35$). For natural streams (b) and (c), the homogeneity-of-slopes test showed a fish × grazer-density interaction in July 1997 ($F_{1,6} = 3.785$, $P = 0.10$) and July 1998 ($F_{1,6} = 9.91$, $P = 0.035$). Regression lines in (b) and (c) were significant in natural fishless streams only (1997, $I_d = -0.0004$[grazer density] + 1.65, $r^2 = 0.81$, $F_{1,3} = 13.00$, $P = 0.037$; 1998, $I_d = -0.0005$[grazer density] + 1.95, $r^2 = 0.89$, $F_{1,2} = 17.83$, $P = 0.052$). There was no relationship between algal I_d and grazer density in trout streams (1997, $r^2 = 0.23$, $F_{1,3} = 0.85$, $P = 0.43$; 1998, $r^2 = 0.09$, $F_{1,2} = 0.20$, $P = 0.70$). Total grazers included caddisflies and mayflies in panel (a), but only mayflies in panels (b) and (c). Note the different axis scales.

quality food patches (Kohler 1984, Peckarsky 1996), and, like other stream grazers (e.g., Lamberti and Resh 1983, Power 1987, Gelwick and Matthews 1997), their grazing has the potential to reduce the abundance of high quality resource patches, thereby reducing the contrast between high and low resource patches. Selective grazing, whereby grazing reduces the contrast between resource patches, is known to decrease resource heterogeneity of terrestrial vegetation when grazers closely track variations in patch quality (Adler et al. 2001). Similarly, we suspect that the high rate of movement and strong patch selection, especially by *Baetis*, played an important role in decreasing algal heterogeneity in fishless situations.

Although these experiments were not designed to test the precise mechanisms causing observed responses, we present two non-mutually exclusive mechanisms that could explain higher algal heterogeneity in the presence of trout odor. First, predators by constraining grazer behavior may force grazers to stay in particular patches longer, grazing them down more, while allowing ungrazed patches to increase in abundance. Although grazers in fish odor mesocosms spent more time in fast than slow flow patches during the day, algal biomass did not differ between rocks in fast and slow flow areas. Thus, our observations do not support this mechanism to explain increased algal heterogeneity in trout mesocosms.

However, predators can affect a variety of prey behavior including movement rate, patch residence time, and other aspects of microhabitat selection (Lima 1998). Thus, we cannot rule out this mechanism without a more detailed, mechanistic study of predator-induced changes in microhabitat selection and differential grazing of patches. For example, grazers may become more choosey about aspects of rock size, overhangs, texture, or color leading to differential grazing of individual rocks in the presence of fish odor. In other words, algal heterogeneity could be higher in risky environments because of high algal densities on rocks with poor predator protection and low algal densities on rocks with good predator protection.

This mechanism is also consistent with theoretical predictions that, for highly mobile consumers that graze resource patches faster than resource growth rate, resource heterogeneity should increase if predators reduce consumer movement (Abrams 2000). However, Abrams' (2000) models assume no spatial differences in predator protection among different resource patches, as may be the case in stream habitats. Thus, in the model, predators increase resource heterogeneity by

increasing the time (by reducing movement) for grazers to find high resource patches.

A second plausible mechanism explaining results of experiments is that by constraining grazer movement, trout reduced consumer influence on resource heterogeneity allowing physical habitat variation (e.g., microhabitat differences in current and substratum) to have an overriding influence on algal heterogeneity. Under this scenario, grazers decrease heterogeneity in fishless streams and physical factors increase heterogeneity in fish streams where grazer behavior is suppressed. We observed more grazer activity on the tops of rocks in fishless treatments of both mesocosm and whole-stream experiments, and have previously observed increased grazer movement (drift) in fishless mesocosms and natural streams (McIntosh et al. 2002). Thus, under this scenario predators prevent grazers from accessing high resource abundance patches, thereby preventing them from homogenizing resource variability caused by the physical environment. The higher resource heterogeneity in the mesocosms lacking grazers compared to those with grazers in the mesocosm experiment supports the hypothesis that physical factors increase resource heterogeneity, which is subsequently reduced by grazing.

The effects of consumers on resource heterogeneity depend on the scale of observations, the spatial arrangement of resources, and the abundance of consumers (Poff and Nelson-Baker 1997, Abrams 2000, Adler et al. 2001). The results of our survey from natural streams indicate that variations in grazer density may have an important influence on resource heterogeneity. We suspect that relatively low densities of grazers in some naturally fishless streams (vs. fish streams; see Table 2) were not sufficient to homogenize the distribution of algal resources in natural fishless streams, which could be why we did not observe differences in resource heterogeneity between fish and fishless streams (Fig. 3c). We observed significant effects of grazers on algal heterogeneity only in controlled experiments using equal or similar grazer densities (Fig. 3a and b). Furthermore, the lack of association between grazer densities and algal heterogeneity in the whole stream experiment (Fig. 5a) could be attributed to dilution of mayfly effects in these headwater streams by grazing cased caddisflies, which are less vulnerable to drift-feeding fishes and less mobile than mayflies (Wootton et al. 1996).

Our results from natural streams demonstrate that the presence of predators can decouple the relationship between grazer density and resource heterogeneity. Other studies have demonstrated that increases in the abundance of grazers can homogenize their resources, but have not considered the role of predators in this relationship. For example, Sarnelle et al. (1993) observed a decrease in the spatial variability of filamentous algae (*Cladophora*) with an increase in the density of grazing snails in experimental channels. Flecker and Taylor (*unpublished manuscript*) observed that at intermediate densities grazing catfish increased resource (organic sediment) spatial heterogeneity in neotropical streams by removing sediment from patches, thereby interrupting an otherwise homogeneous cover. However, further increases in catfish density reduced heterogeneity by removing sediment resulting in a homogeneous distribution of low resource abundance.

In summary, we suspect that the mechanisms explaining observed indirect effects of predators on resource heterogeneity involved: (1) selective grazing of high quality resources by consumers combined with predator-induced changes to microhabitat selection, or predator-inflicted constraints on grazer movement to high quality resource patches, and (2) differences in resource abundance caused by the physical environment. Furthermore, indirect effects of predators on resource heterogeneity may also be influenced by grazer densities.

We speculate that top-down interactions will result in changes in resource distributions rather than resource abundance if the background environment is characterized by high habitat variability and predators have strong, trait-mediated (as opposed to density mediated) effects on grazers (Peacor and Werner 2000). In heterogeneous environments such as streams, which also provide refuges for grazers from predation (Power 1992, Hildrew and Giller 1994), predators may be more likely to influence the heterogeneity of primary producers, potentially explaining why conventional trophic cascades (based on mean abundance) are generally weak in streams (Shurin et al. 2002). In our study, mean algal abundance in fish and fishless streams was not significantly different in the mesocosm and whole-stream experiments, whereas predator-induced changes in consumer behavior caused differences in resource distribution. Although high densities of grazers and low biomass of algae were observed in natural trout streams (Table 2), we cannot attribute these patterns to a conventional trophic cascade, because predation by trout could not cause the observed differences in grazer densities (B. L. Peckarsky, *unpublished manuscript*).

We anticipated that predator-mediated effects on resource heterogeneity would be more apparent in smaller, simpler systems with fewer uncontrolled variables that could affect grazer and algal distributions. The mesocosm experiments included only one species of grazer at controlled densities and controlled abiotic conditions, potentially increasing the probability of detecting effects of predators. The manipulated stream reaches had very similar abiotic conditions, but somewhat different densities and more than one species of grazer (Peckarsky et al. 2002). Nonetheless, we were also able to observe a significant influence of predation risk on the distributions of grazers and their resources in these small natural streams. It is also important to note that the responses observed in both experiments were to trout chemical cues. In large natural systems,

chemical cues may behave differently, and the full range of predator cues (i.e., visual and hydrodynamic) may elicit a different response. In more complex systems, multiple interacting factors affecting algal resource distributions (e.g., variations in grazer densities, resource growth rates, and the physical environment) may also obscure some of the patterns detectable at smaller scales and in simpler systems (Peckarsky et al. 1997). Nevertheless, we have demonstrated that predator-prey interactions can play an important role in the generation and maintenance of spatial resource heterogeneity, and our findings emphasize the importance of considering heterogeneity as an integral part of natural ecological systems and a important product of interspecific interactions.

ACKNOWLEDGMENTS

We thank Marge Penton, Tracy Smith, Dewey Overholser, Chester Anderson, John Larison, Jonas Dahl, Bryan Horn, and Alison Horn for help in the field and laboratory. We thank Don and Margaret Bailey, who kindly gave access to streams on their land, and the staff at the Rocky Mountain Biological Laboratory for their support. Comments from Jon Harding, Per Nyström, Hamish Greig, Mike Winterbourn, Peter Abrams, Barbara Downes, and two anonymous reviewers improved the manuscript. This research was supported by NSF grant DEB-9629404 to B. L. Peckarsky and A. R. McIntosh and funding from the University of Canterbury to A. R. McIntosh.

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