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EXCLUSION EXPERIMENTS WITH BACKWATER INVERTEBRATE COMMUNITIES OF THE GREEN RIVER, UTAH

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ABSTRACT.—The role of biotic interactions in structuring freshwater invertebrate communities has been extensively studied but with mixed results. For example, fish effects on invertebrates are most pronounced in pelagic and soft-sediment benthic habitats that lack structural complexity, yet appear insignificant in benthic rubble habitats. Backwaters of the Green River, Utah, are shallow, structurally simple, quiet-water embayments adjacent to the river. These habitats form in middle to late summer and are colonized by benthic and epibenthic invertebrates that produce standing crops significantly higher than the river. Backwaters are also utilized by a large number of fish species. We used cages to determine if selective exclusion of backwater organisms could significantly change invertebrate community structure. Results showed that backwater invertebrate community components changed significantly in response to exclusion treatments. Two taxa (both predators), the chironomid genus *Tanypus* (Diptera: Chironomidae) and the corixid genus *Trichocorixa* (Hemiptera: Corixidae), increased in density in exclusion cages while cladocerans, immature copepods, the cyclopoid copepod *Eucyclops speratus*, and the chironomid genus *Procladius* all decreased in density. Diversity of adult copepods was reduced by exclusion treatments, though density of only a single species changed significantly.

Key words: predation, backwater, invertebrate communities, Green River, Colorado River drainage, cage effects.

The impact of predation on density and diversity of aquatic invertebrate prey is unclear and seems to depend on habitat type. Investigations of freshwater pelagic habitats have revealed that predator-induced trophic cascades can be a driving force (Carpenter et al. 1987). In these structurally simple habitats, both vertebrate and invertebrate predators can have a profound effect on the density and diversity of zooplankton (Brooks and Dodson 1965, O'Brien 1979, Sih et al. 1985, Carpenter et al. 1987, Kerfoot and Sih 1987). However, studies of freshwater benthic communities have had mixed results. Streams with stony substrates generally fail to show significant effects of vertebrate predators on benthic invertebrate density or diversity (Reice 1983, Flecker and Allan 1984, Reice and Edwards 1986). Conversely, invertebrates in soft-sediment stream habitats respond to variations in fish predation (Wilzbach et al. 1986, Gilliam et al. 1989, Schlosser and Ebel 1989). It has been suggested that the structural complexity of stony substrates offers greater refuge from predation than soft, silty substrates (Allan 1983, Gilliam et al. 1989) where predators have greater access to invertebrate prey.

Ephemeral backwaters of the Green River are shallow, sand- and silt-bottomed habitats. At least 8 native and 15 nonnative fish species are found in these backwaters from midsummer through autumn (Haines and Tyus 1990); most abundant are nonnative red shiners (*Cyprinella lutrensis*) and fathead minnows (*Pimephales promelas*), and native Colorado pikeminnow (*Ptychocheilus lucius* [Haines and Tyus 1990, K.P. Collins unpublished data]). Muth and Snyder (1995) found that Green River backwater fish diets mainly consist of Diptera larvae, copepods, cladocerans, rotifers, corixids, nematodes, and fish.

Based on structural simplicity of backwater habitats, we hypothesized that manipulation of fish access would impact invertebrate community density and diversity. An exclusion experiment was designed and performed to test this hypothesis.

METHODS

Study Area

The Green River (Colorado River drainage) originates in Wyoming and joins the Colorado River in southeastern Utah. It enters our study

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area at Ouray National Wildlife Refuge (ONWR) 404 km above the Colorado River confluence. At Jensen, Utah (near ONWR), it has a 47,723-km^2 drainage area with average peak flow of 338 m^3 s^{-1} and average low flow of 106 m^3 s^{-1} (U.S. Geological Survey data). Backwaters are cut off secondary side channels and quiet-water habitats isolated behind point bars that emerge as river level falls in summer; the length of backwaters is greater than the width at their mouth. Backwaters in this study were shallow (approximately 0.75 m to 1.0 m deep) with no current. Secchi disk visibility averaged 22 cm, and substrate was soft sediments under a flocculent layer approximately 4 cm thick. Backwaters were free of macrophytes. Lack of current and relatively stable substrate allow backwaters to support higher invertebrate density than the main river (Mabey 1993, Wolz and Shiozawa 1995). Combination of high food concentration, warmer temperatures, and no current is likely what makes backwaters attractive to fish.

Experimental Design

A 3-way analysis of variance design was used with the following 3 treatments in each of 3 replicate backwaters sampled over a 4-month period: (a) control—a cageless (2 × 2-m) area, marked by posts, which was open for foraging to all backwater organisms; (b) closed—a caged area (2 × 2-m) that excluded all fish and large, nonflying invertebrates; and (c) perforated—a cage (2 × 2-m) with 2.5-cm-wide by 10-cm-high perforations (approximately 10 cm apart) in each side for a total of approximately 80 perforations per side. Perforations excluded adult carp (*Cyprinus carpio*) and channel catfish (*Ictalurus punctatus*), but not smaller fish, such as young Colorado pikeminnow, red shiner, and fathead minnow, and large invertebrates. Each cage panel was 1.2 m high and 2 m wide, framed with wood, and covered with 1.6-mm fiberglass screen mesh. Panels were bolted together and secured with fence posts at each corner. Cages extended 20–40 cm above water, varying with river depth. Treatment position within each backwater was randomized.

Sampling

We installed cages 6–8 August 1992 and took samples 14–15 August (week 1), 28–29 August (week 3), and 11–12 September (week 5). Each sample comprised 30 benthic cores (19-mm diameter, 10-cm depth) and 5 vertical plankton tows (20-cm diameter, 63-μm mesh) from each treatment within each backwater. Over the duration of the experiment, we took a total of 180 core samples per treatment, and total area sampled was approximately 510 cm^2. Samples were preserved in 5% formalin.

Core samples were washed through a 63-μm mesh screen. Diptera larvae (Chironomidae and Ceratopogonidae), Cladocera, Copepoda (adults, copepodites, and nauplii), Rotifera, Corixidae, Nematoda, Oligochaeta, and Gastrotricha were counted from at least 10 benthic cores randomly chosen from 30 cores from each treatment/backwater combination on each date. We counted organisms from all 5 plankton tows, and all cladocerans and adult copepods from those samples were identified. Chironomidae were mounted on slides in Hoyer's solution and identified to genus using Mason (1968), Wiederholm (1983), and Merritt and Cummins (1984). Cladocerans and adult copepods were identified to species using keys by Yeatman (1959) and Pennak (1989).

Statistical Analysis

Data were examined with weighted 3-way analysis of variance (ANOVA) tests on means of log-transformed (ln [x + 1]) sample counts for each group of organisms. The ANOVA model was:

$$Y_{ijk} = \mu + B_i + T_j + BT_{ij} + D_k + BD_{ik} + TD_{jk} + BTD_{ijk}$$

where Y_{ijk} is the log-transformed mean of subsample counts from the j^{th} treatment in the i^{th} backwater on the k^{th} date, B_i is the random backwater (block) effect, T_j is the fixed treatment effect, and D_k is the fixed date effect. Treatment effects *F*-ratios were calculated using the mean square of the block by treatment interaction as the denominator. Anderson-Darling normality tests showed that in all cases data were normal.

We analyzed effects of fish predation on richness, evenness, and heterogeneity of chironomids and copepods using the same ANOVA design. Chironomids and planktonic copepods were used to test for diversity effects because they are readily identified to genus and species, respectively. We calculated richness, evenness, and heterogeneity for each treatment replicate on each date. Species richness was based on the rarefaction method

(Hurlbert 1971, Simberloff 1972), which estimates the number of species expected in a random sample of n individuals taken from a collection. Heterogeneity was estimated with the nonparametric Simpson's reciprocal index (Hill's N_2; Hill 1973). Evenness was calculated using the modified Hill's ratio (Alatalo 1981).

Mean densities and 95% confidence intervals of major benthic and planktonic invertebrate taxa were calculated for each treatment on each date. Plankton densities were calculated on ln (x + 1) transformed count data and then converted back into actual densities because of small sample size and a negative binomial distribution (Elliot 1977).

RESULTS

Benthic Invertebrate Densities

Four benthic taxa showed significant treatment effects. The chironomid genera *Tanypus* and *Procladius* were significantly affected by treatment (3-way ANOVA, treatment effect: $F_{2,4} = 30.95$, $P = 0.004$; $F_{2,4} = 9.08$, $P = 0.033$, respectively; Figs. 1b, 1c), and total numbers of immature chironomid (Diptera) larvae showed a marginal treatment effect (3-way ANOVA, treatment effect: $F_{2,4} = 5.85$, $P = 0.064$; Fig. 1a). *Tanypus* densities were lower in open controls than in perforated and closed treatments on week 3 (Tukey pairwise comparisons of treatment effect: $P = 0.025$ for open vs. perforated, and $P = 0.043$ for open vs. closed), but had no significant pairwise differences among treatments in weeks 1 and 5. This is probably due, in week 5, to high variance in *Tanypus* density in open controls. Despite a significant overall treatment effect for *Procladius*, Tukey comparisons showed no pairwise differences among treatments for any date.

The closed-cage treatment reduced the abundance of benthic copepodites (3-way ANOVA, treatment effect: $F_{2,4} = 14.50$, $P = 0.015$; Fig. 2a) and nauplii (3-way ANOVA, treatment effect: $F_{2,4} = 8.50$, $P = 0.036$; Fig. 2b) relative to controls. Tukey pairwise comparisons revealed that on week 3 copepodite densities in controls were significantly higher than in closed treatments ($P = 0.015$), and on week 5 control densities were marginally higher than both perforated and closed treatments ($P = 0.092$ for open vs. perforated, and $P = 0.079$ for open vs. closed). Nauplii densities in perforated (though not control) treatments were significantly higher than in closed treatments on week 3 ($P = 0.05$), and control densities were marginally higher than closed treatments on week 5 ($P = 0.07$). In most cases copepodites and nauplii densities in perforated treatments were intermediate between control and closed densities (Fig. 2).

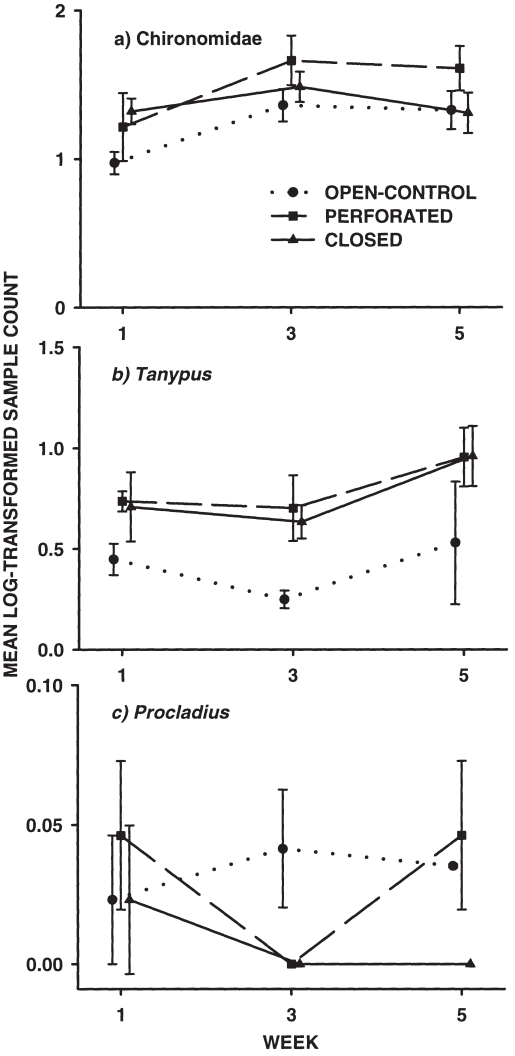

Fig. 1. Mean of average log-transformed sample counts from benthic cores used in 3-way ANOVA for (a) Chironomidae, (b) *Tanypus*, and (c) *Procladius* from Green River backwaters, Ouray National Wildlife Refuge, Utah. Vertical bars indicate ±1 *s*; $n = 3$ for each treatment/date combination.

Only Oligochaeta and Chironomidae (total) showed significant treatment by date interactions (3-way ANOVA, treatment by date

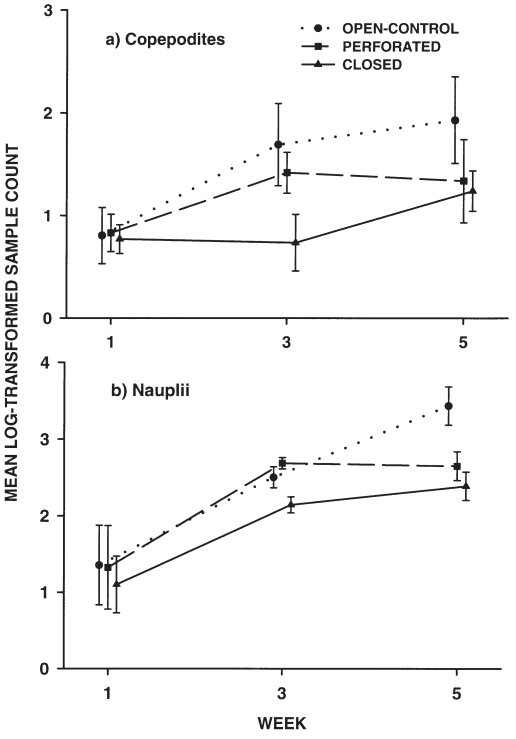

Fig. 2. Mean of average log-transformed sample counts from benthic cores used in 3-way ANOVA for (a) copepodites and (b) nauplii from Green River backwaters, Ouray National Wildlife Refuge, Utah. Vertical bars indicate ±1 *s*; $n = 3$ for each treatment/date combination.

interaction: $F_{4,8} = 4.17$, $P = 0.041$; $F_{4,8} = 4.91$, $P = 0.027$, respectively). Nematodes, the most abundant benthic taxon, showed no significant treatment effect or treatment by date interaction (Table 1).

Planktonic Invertebrate Densities

Four planktonic taxa showed significant or marginally significant treatment effects, but none showed a significant treatment by date interaction. Of the 4, only *Trichocorixa* (Hemiptera: Corixidae) had higher densities in closed cages relative to controls (3-way ANOVA, treatment effect: $F_{2,4} = 15.93$, $P = 0.012$; Fig. 3a). As with *Tanypus, Trichocorixa* densities were similar in perforated and closed treatments. Tukey pairwise comparisons showed that *Trichocorixa* density in controls was marginally lower than in perforated treatments on week 1 ($P = 0.07$), and significantly lower than perforated and closed treatments on week 3 ($P = 0.039$ for open control vs. perforated, and $P = 0.018$ for open control vs. closed). The 3 treatments did not differ in week 5, probably due to large variance around means of perforated and closed treatments on that week.

Three planktonic microcrustacean groups had decreased numbers in closed cages relative to controls. Number of cyclopoid copepod *Eucyclops prionophorus* (3-way ANOVA, treatment effect: $F_{2,4} = 8.53$, $P = 0.036$; Fig. 3b) and total cladocerans (3-way ANOVA, treatment effect: $F_{2,4} = 11.93$, $P = 0.021$; Fig. 3c) showed significant treatment effects, and number of copepod nauplii showed a marginally significant effect (3-way ANOVA, treatment effect: $F_{2,4} = 4.46$, $P = 0.096$; Fig. 3d). The trend in all 3 cases was for controls to have higher densities than closed treatments (Fig. 3). However, Tukey pairwise comparisons of *E. prionophorus* showed no significant differences among treatments on any sampling date, and only marginally significant differences for nauplii on week 5 ($P = 0.054$ and $P = 0.096$ for open control vs. perforated and closed treatments, respectively). Pairwise comparisons of cladoceran treatment means revealed that numbers in closed treatments were significantly lower than in controls on week 3 ($P = 0.07$), but there were no significant differences among treatments for weeks 1 and 5. Cladoceran density declined steadily over the study period. However, their abundance decreased more rapidly in closed treatments than in controls (Fig. 3b). Cladocerans in perforated treatments were intermediate between controls and closed during weeks 3 and 5 (Fig. 3b).

Immature copepods (copepodites and nauplii) and rotifers were the most abundant planktonic groups (Table 2). Four copepod species (*Eucyclops speratus*, *Eucyclops prionophorus*, *Acanthocyclops vernalis*, and *Diacyclops bicuspidatus*, although *A. vernalis* and *D. bicuspidatus* were in low numbers [Tables 1, 2]) and 3 cladoceran species (*Ilyocryptus sordidus*, *Macrothrix laticornis, Leydigia quadrangularis*) were collected in plankton samples (Table 2). Of these, only *L. quadrangularis,* represented by just 3 specimens, did not also occur in benthic samples.

Diversity

At least 4 species of cyclopoid copepods were present in the backwaters (see above). There was a significant treatment effect on

TABLE 1. Average density (number · m^{-2}) and 95% confidence intervals for major benthic invertebrate taxa in core samples, Green River backwaters, Ouray National Wildlife Refuge, Utah. Average densities calculated by pooling core sample data from all 3 sites for each treatment/date combination.

	Week 1			Week 3			Week 5		
Taxon	Control	Perforated	Closed	Control	Perforated	Closed	Control	Perforated	Closed
Nematoda	140683 ± 18388	142697 ± 23597	133294 ± 24089	211296 ± 37067	185561 ± 33001	178556 ± 27473	221682 ± 37313	243024 ± 35731	211129 ± 34589
Oligochaeta	3244 ± 1343	13268 ± 3829	5800 ± 1573	30068 ± 6917	23621 ± 4850	17961 ± 4454	30999 ± 8079	41604 ± 10174	16260 ± 3464
Ceratopogonidae	203 ± 262	120 ± 134	510 ± 458	860 ± 442	396 ± 258	487 ± 281	208 ± 212	452 ± 292	688 ± 388
Chironomidae	7825 ± 1484	11344 ± 1855	11993 ± 1709	13808 ± 3069	17795 ± 2354	15326 ± 2655	12449 ± 2151	16235 ± 2172	13543 ± 2640
Chironomus spp.	2709 ± 788	3880 ± 1381	3527 ± 1367	3410 ± 986	5761 ± 1800	5291 ± 1473	3408 ± 945	5056 ± 1508	3892 ± 1429
Tanypus spp.	2772 ± 893	4938 ± 1610	4821 ± 1606	1411 ± 597	4821 ± 1830	4115 ± 1448	3707 ± 1255	7055 ± 1904	7298 ± 1999
Procladius spp.	126 ± 173	235 ± 320	118 ± 230	235 ± 278	0	0	179 ± 199	235 ± 320	0
Adult Copepoda	2277 ± 716	4468 ± 1783	3292 ± 2068	4689 ± 1470	5056 ± 2265	3527 ± 1373	8217 ± 1760	5526 ± 2603	7839 ± 4234
Eucyclops speratus	1875 ± 595	4115 ± 1558	3175 ± 2079	3871 ± 1345	5173 ± 2192	3162 ± 1344	6383 ± 1750	4586 ± 2655	5226 ± 3261
E. prionophorus	223 ± 288	353 ± 385	0	559 ± 281	0	122 ± 238	1680 ± 517	706 ± 611	2352 ± 1930
Acanthocyclops vernalis	134 ± 150	0	0	43 ± 84	0	122 ± 238	126 ± 141	0	0
Diacyclops bicuspidatus	45 ± 88	0	118 ± 230	0	0	122 ± 238	0	0	0
Copepodites	6422 ± 1810	6232 ± 2191	5644 ± 1921	24691 ± 5100	15755 ± 4766	5960 ± 3328	32244 ± 6553	16343 ± 7917	12280 ± 4903
Nauplii	20434 ± 6766	23208 ± 7978	12855 ± 3834	53985 ± 9161	61391 ± 8742	39084 ± 7647	132752 ± 16699	78234 ± 24074	76526 ± 23165
Cladocera	4879 ± 1443	5050 ± 1430	7564 ± 2559	3570 ± 1160	4360 ± 1326	4298 ± 1535	3112 ± 771	2668 ± 839	2022 ± 848
Ilyocryptus sordidus	2998 ± 1199	7407 ± 3203	6584 ± 3761	2961 ± 1116	3762 ± 2015	3892 ± 2259	3065 ± 2177	2704 ± 1394	2394 ± 1707
Macrothrix laticornis	176 ± 170	470 ± 548	0	436 ± 282	0	0	798 ± 395	1058 ± 822	252 ± 358
Gastrotricha	3649 ± 1436	15071 ± 8193	4468 ± 3141	41640 ± 14941	22670 ± 5803	23962 ± 7621	57060 ± 14882	87234 ± 25093	59377 ± 14442
Rotifera	3000 ± 1039	6774 ± 3200	2665 ± 909	10539 ± 2662	11573 ± 2436	8717 ± 1977	12532 ± 2896	14019 ± 3715	10883 ± 2712

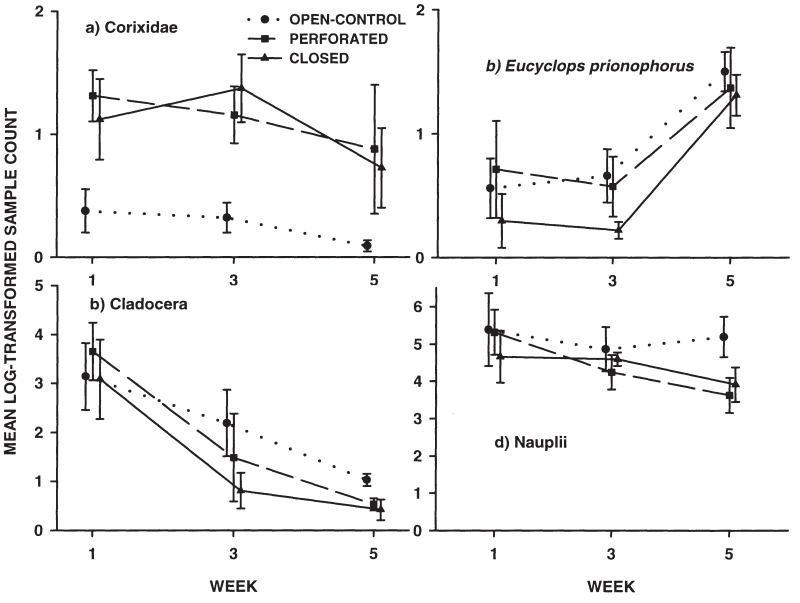

Fig. 3. Mean of average log-transformed sample counts from vertical plankton tows used in the 3-way ANOVA for (a) Corixidae, (b) *Eucyclops prionophorus*, (c) Cladocera, and (d) nauplii from Green River backwaters, Ouray National Wildlife Refuge, Utah. Vertical bars indicate ±1 *s*; $n = 3$ for each treatment/date combination.

heterogeneity and evenness (3-way ANOVA, treatment effect: $F_{2,4} = 11.27$, $P = 0.023$; $F_{2,4} = 13.57$, $P = 0.016$, respectively; Figs. 4a, 4b), and a marginally significant effect on species richness of planktonic copepods (3-way ANOVA, treatment effect: $F_{2,4} = 6.42$, $P = 0.056$; Fig. 4c). All 3 measures showed a trend of decreased copepod diversity in perforated and closed cages. Tukey pairwise comparisons showed a significant effect on species richness between controls and closed treatments ($P = 0.05$) and a marginally significant effect between perforated and closed treatments ($P = 0.08$) on week 3, but no pairwise differences on weeks 1 or 5. Heterogeneity showed a marginally significant effect between perforated and closed treatments on week 1 ($P = 0.097$) and between controls and closed treatments on week 5 ($P = 0.10$). Pairwise comparisons of treatment effects on heterogeneity between controls and perforated were significant for week 5 ($P = 0.025$). Pairwise comparisons of treatment effects on evenness between controls and closed cages were marginally significant on week 3 ($P = 0.098$) and significant on week 5 ($P = 0.028$). Controls and perforated treatments also showed significant differences for evenness on week 5 ($P = 0.009$).

We collected 10 chironomid genera in the benthos: *Chironomus, Glyptotendipes, Cryptochironomus, Polypedilum, Stempellinella, Nimbocera, Tanytarsus, Lenziella, Tanypus,* and *Procladius.* Only *Chironomus* and *Tanypus* were abundant. Abundances of *Tanypus* and *Procladius* were significantly affected by treatments. There was no treatment effect on any of the diversity measures for chironomids.

DISCUSSION

Density Effects

Two taxa, the chironomid genus *Tanypus* and the corixid genus *Trichocorixa,* had increased abundances in closed-cage treatments. Higher densities in closed treatments could be caused by increased survivorship due to absence of fish predators, favorable conditions created by the cage, or increased immigration/decreased emigration in the cage. Patterns in Figures 1b and 3a do not rule out any of these possibilities. Average number of organisms in perforated cages is indistinguishable from closed cages in both cases. This pattern suggests that either few fish entered the perforated cages or those that entered did not prey upon *Tanypus* and *Trichocorixa.*

TABLE 2. Average density (number · m^{-2}) and 95% confidence intervals for major planktonic invertebrate taxa in vertical plankton tows, Green River backwaters, Ouray National Wildlife Refuge, Utah. Averages were calculated by pooling vertical plankton tow data from all 3 sites for each treatment/date combination.

Taxon	Week 1			Week 3			Week 5		
	Control	Perforated	Closed	Control	Perforated	Closed	Control	Perforated	Closed
Adult Copepoda	96 ± 5	150 ± 5	173 ± 7	97 ± 6	125 ± 6	157 ± 4	81 ± 3	56 ± 5	60 ± 7
Eucyclops speratus	79 ± 5	115 ± 6	135 ± 9	85 ± 7	108 ± 7	146 ± 4	41 ± 3	21 ± 7	32 ± 8
E. prionophorus	5.6 ± 2.7	8.0 ± 4.4	3.1 ± 2.8	6.5 ± 3.3	5.7 ± 2.7	2.0 ± 2.0	29 ± 5	23 ± 4	22 ± 3
Acanthocyclops vernalis	5.4 ± 4.0	5.8 ± 4.3	8.5 ± 7.3	2.7 ± 2.6	5.5 ± 4.3	1.3 ± 1.5	2.0 ± 2.3	0.77 ± 1.1	1.4 ± 1.7
Diacyclops bicuspidatus	1.5 ± 1.8	5.3 ± 4.3	4.7 ± 3.3	0	0	0	0	0	0
Copepodites	322 ± 6	505 ± 4	345 ± 6	532 ± 11	193 ± 8	228 ± 6	336 ± 5	128 ± 3	120 ± 4
Nauplii	1518 ± 11	1627 ± 7	861 ± 9	1022 ± 6	547 ± 6	781 ± 4	1536 ± 5	291 ± 6	392 ± 5
Cladocera	191 ± 8	315 ± 8	144 ± 13	63 ± 8	27 ± 11	9.8 ± 6.1	14.4 ± 2.8	5.5 ± 3.3	4.1 ± 5.1
Ilyocryptus sordidus	123 ± 13	174 ± 16	55 ± 26	50 ± 14	25 ± 12	8.0 ± 6.6	4.1 ± 3.1	3.4 ± 4.9	2.7 ± 7.0
Macrothrix laticornis	7.3 ± 5.6	14.3 ± 7.5	7.3 ± 6.7	4.6 ± 3.2	1.9 ± 1.7	2.2 ± 2.3	6.4 ± 3.0	1.2 ± 1.7	2.1 ± 5.1
Corixidae	3.4 ± 2.3	21 ± 5	17.6 ± 6.3	3.0 ± 2.2	17.3 ± 4.7	23 ± 6	0.83 ± 1.2	11.2 ± 4.9	8.5 ± 3.4
Rotifera	2652 ± 13	1890 ± 16	5291 ± 40	226 ± 3	201 ± 4	265 ± 6	331 ± 4	306 ± 2	426 ± 3
Gastrotricha	2.9 ± 3.0	11.3 ± 14.3	6.8 ± 5.9	6.2 ± 2.6	3.2 ± 3.3	3.1 ± 4.1	8.8 ± 4.6	0.38 ± 0.83	2.3 ± 1.9

Fig. 4. Mean values of diversity measures for copepods collected in vertical plankton tows and used in 3-way ANOVA of (a) heterogeneity, (b) evenness as measured by the modified Hill's ratio, and (c) species richness estimated using rarefaction method, from Green River backwaters, Ouray National Wildlife Refuge, Utah. Vertical bars indicate ±1 *s;* $n = 3$ for each treatment combination.

Trichocorixa and *Tanypus* are large (relative to other backwater invertebrates) predators and may have been depleted by fish through size-selective predation. However, *Chironomus*, a detritivore, was more abundant and larger than *Tanypus*, and yet appeared unaffected by treatments. This suggests that if lower density of *Tanypus* in controls was the result of fish predation, then it is more likely attributable to behavior than size. Studies show that predatory chironomids are more susceptible to fish predation. For example, Gilinsky (1984) found that the dominant predatory midge in a pond was most affected by fish predation, Goyke and Hershey (1992) observed that Arctic ponds without fish had a significantly higher proportion of predaceous chironomids than ponds with fish, and Macchiusi and Baker (1991) showed that size-selective predation on midges can be explained by differential activity of the midges. Spatial distribution of midges may also be important in their susceptibility to fish predation. For instance, in soft benthic sediments of Utah Lake more than 85% of larval *Tanypus stellatus* occur within the top 2.5 cm of sediments, but only 33% of larval *Chironomus frommeri* are found in the same zone (Shiozawa and Barnes 1977).

Differential migration rates between the inside and outside of cages may also help explain our results. First and 2nd instar *Trichocorixa* are small enough to fit through the exclosure mesh, and 76% of individuals we measured were 1st or 2nd instars. It thus is possible that elevated numbers of corixids in perforated and closed treatments were the result of immigration. However, the few *Trichocorixa* caught in controls were early instars as well. It is unclear whether increased density of *Trichocorixa* in cages was a result of increased survivorship or immigration. As for *Tanypus*, it seems more likely that increased survivorship played a larger role since they are less mobile than *Trichocorixa* and therefore less likely to migrate into cages.

We did not find significant evidence of direct effects of exclusion on copepods, cladocerans, or nematodes although all 3 are in the diets of backwater fishes (Muth and Snyder 1995). Studies of predation on benthic invertebrates have attributed similar results to compensatory predation from invertebrate predators (Crowder and Cooper 1982, Cooper et al. 1990, Diehl 1992). This is further supported by a meta-analysis indicating that benthic invertebrate predators have more than twice the impact on other benthic invertebrates that vertebrate predators do (Wooster 1994). Cladocerans, copepodites, and nauplii in our study all had greater abundances in controls than in closed cages.

Closed-cage treatments had a negative effect on 4 taxa: *Procladius*, *Eucyclops prionophorus*, immature Copepoda (both copepodites and nauplii), and Cladocera. One explanation of this effect is increased levels of invertebrate predators like *Trichocorixa* and *Tanypus* in closed treatments. Both feed on benthic organisms, making it possible that they reduced the number of immature copepods and *Procladius*. However, *E. prionophorus* and cladocerans showed a significant treatment effect for individuals in plankton tows only. This makes it more likely that they were affected by *Trichocorixa*, which feeds in the water column as well as benthos. No invertebrate predator effect on oligochaetes was detected even though predatory and omnivorous chironomids (such as *Tanypus* and *Chironomus*), as well as *Trichocorixa*, are known oligochaete predators. However, since uneaten portions of oligochaetes can often regenerate, their biomass may decrease in the presence of predators while their overall numerical density remains the same (Loden 1974, Wisniewski 1978).

Other possibilities to explain the lower numbers of some taxa in closed-cage treatments include decreased survivorship due to less favorable conditions within cages, and lower rates of immigration. Patterns in Figures 1–3 do not rule out any of the possible scenarios but may give some insight. Figures 2a, 2b, 3b, and 3c all indicate that densities in perforated cages were intermediate to those in closed treatments and controls. Fish may have entered perforated cages and reduced the number of invertebrate predators, which increased survivorship of some taxa relative to the closed treatment. If this is the case, then the difference in abundance between control and closed areas might represent an indirect effect of fish predation (i.e., fish decrease invertebrate predators which indirectly benefits prey of those predators). Another possibility is that perforated cages allowed greater access to some taxa than closed treatments, or physical

conditions in perforated treatments were intermediate to those in controls and closed treatments. If either is true, then lower numbers of some taxa in closed cages may simply be an artifact of the cages.

Diversity Effects

The heterogeneity, evenness, and possibly species richness of planktonic copepods appear enhanced in open water, and yet only a single species showed any density differences. It is possible that compensatory predation by invertebrate predators, in closed cages, equalized densities of copepods in the controls and closed treatments but did not have the same impact as fish on copepod diversity. Another possibility is that as rare species were recruited into the backwaters, they were unable to gain access to the closed cages, thereby lowering diversity. However, we believe this was not the case since Figure 4a clearly shows that controls and closed cages follow the same upward and downward trends. More specifically, the increase in heterogeneity from week 3 to week 5 in the open control as well as the closed treatments indicates that at least some of the rare species appearing in the backwaters were also recruited into the closed treatments.

Two chironomid taxa, *Tanypus* and *Procladius,* showed significant treatment effects on density, but we were unable to find significant treatment effects on chironomid diversity. We identified chironomids to generic level, which may have been too coarse a scale for diversity questions, and chironomid community diversity may have required more time to respond to treatments than the copepod community (Diehl 1992). In addition, the structural complexity of the benthic substrate may allow for a fairly diverse (11 genera) community that is not significantly affected by predation (Gilinsky 1984).

The impact of predation on density and diversity of invertebrates seems to depend on habitat type. Our results suggest that backwater fish communities of the Green River may significantly impact several invertebrate taxa. However, with our design we were unable to distinguish between fish effects and other effects created by treatment cages. Future studies will be required to separate these effects and more completely address the role of predation in structuring Green River backwater invertebrate communities.

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