

Reports

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AN EXPERIMENTAL DISTURBANCE ALTERS FISH SIZE STRUCTURE BUT NOT FOOD CHAIN LENGTH IN STREAMS

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Abstract. Streams experience frequent natural disturbance and are undergoing considerable anthropogenic disturbance due to dam construction and water diversion. Disturbance is known to impact community structure, but its effect on food chain length is still a matter of considerable debate. Theoretical models show that longer food chains are less resilient to disturbance, so food chain length is predicted to be shorter following a disturbance event. Here we experimentally test the effect of disturbance on food chain length in streams by diverting stream flow. We found that our experimental low-flow disturbance did not alter food chain length. We did see an effect on body-size structure in our food webs suggesting that food chain length may be an insensitive indicator of disturbance. We suggest that habitat heterogeneity and food web complexity buffer the effect of disturbance on food chain length. The theoretical predictions of disturbance on food chain length are only likely to be seen in homogeneous systems that closely approximate the linear food chains the models are based upon.

Key words: disturbance; food chain length; food web; stream community; water diversion.

INTRODUCTION

Disturbance is a key force structuring ecological communities (White and Pickett 1985), including those of streams (Resh et al. 1988, Poff et al. 1997, Hart and Finelli 1999). In streams, hydrological disturbance plays an important role as hydrologic regime affects the abundance, distribution, and behavior of stream organisms (Peckarsky et al. 1990b, Wootton et al. 1996, Fausch et al. 2001, Covich et al. 2003). Disturbance events include high-flow events that scour organisms from the substrate (Grimm and Fisher 1989) and low-flow events that dry the stream channel (Lake 2003). The frequency and magnitude of these hydrological disturbance events are likely to increase with climate change (Arnell et al. 1996). In addition, increased diversion of water to meet rising human demands will interact with climate change to exacerbate low-flow events (Vorosmarty et al. 2000). While most ecological studies have focused on floods because they can cause significant mortality of aquatic organisms (Fisher et al. 1982), low-flow events may have similar or greater impacts on stream communities (Boulton et al. 1992, Sabo and Post 2008). This is because low-flow events typically last

longer than floods, increase in intensity with time, and can isolate sections of the stream (Boulton et al. 1992, Lake 2000).

Food chain length is an important characteristic of ecological communities that may be strongly influenced by disturbance. Shifts in food chain length can alter ecosystem function, modify trophic interactions, and affect the biomagnification of contaminants (Carpenter et al. 1987, Cabana and Rasmussen 1994, Post 2002a). The dynamical constraints hypothesis (Pimm and Lawton 1977, Pimm 1982) suggests that longer food chains are less resilient to disturbance and implies that food chain length will be shorter following a disturbance or in frequently disturbed habitats (but see Sterner et al. 1997). Disturbance is also expected to strongly influence food chain length when it results in the loss and slow return of upper trophic levels (Menge and Sutherland 1976, Pimm and Kitching 1987, Spiller et al. 1998).

Previous tests of the effect of disturbance on food chain length have reached mixed conclusions. Experiments in small container habitats show that long food chains are more susceptible to shortening by disturbance and take longer to recolonize after a disturbance (Pimm and Kitching 1987, Jenkins et al. 1992). In streams, studies have found that flood disturbance shortens food chain length (Parker and Huryn 2006), lengthens food chain length (Marks et al. 2000), or has no effect (Townsend et al. 1998). The lack of progress may result

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from the use of differing empirical measures of food chain length (Post 2002b) and the lack of a rigorous experimental field test.

We conducted a large-scale ecosystem manipulation to test the resistance of food chain length to a low-flow disturbance in streams. To simulate disturbance, we modified the hydrological regime of three streams by diverting between 40% and 80% of the water with the amount diverted increasing as the summer progressed to mimic drought conditions (Lake 2000). We then examined how food chain length is influenced by disturbance relative to unmanipulated controls. Finally, we explored food web structural mechanisms that could underlie changes in food chain length including species loss, trophic shifts, and shifts in body size.

METHODS

Study sites

Our study streams were located in Yale Myers Forest, a 3213-ha mixed hardwood forest in Windham and Tolland Counties, Connecticut, USA. We had six stream sites, all second- or third-order perennial streams. The streams are 2–5 m wide and 10–25 cm deep with a gravel-cobble substrate and a pool-riffle morphology.

Water diversion

Of the six streams, three had their flows diverted and three were references. There was no difference in average depth (ANOVA, $F_{1,4} = 0.51$, $P = 0.52$) or pool : riffle ratio (ANOVA, $F_{1,4} = 0.001$, $P = 0.98$) between these two groups, but the reference streams were slightly wider (ANOVA, $F_{1,4} = 7.50$, $P = 0.05$). In each stream we sampled two adjacent 100-m long reaches. In the diverted streams, we diverted water around the lower 100-m stretch of the stream. Water was diverted using wooden weirs that directed flow into pipes and around the experimental stream reach. The upper 100-m reach in the diverted streams served as an undisturbed control. Before we began diverting water (May 2006), there was no significant difference in average width (ANOVA, $F_{1,4} = 0.09$, $P = 0.78$), average depth (ANOVA, $F_{1,4} = 0.18$, $P = 0.69$), or pool : riffle ratio (ANOVA, $F_{1,4} = 0.43$, $P = 0.55$) between the upper and lower reach of the streams to be diverted.

Water was diverted for three and a half months from 12 June until 3 October 2006, although heavy rainfall overwhelmed the structures in late June so no water was diverted from 25 June to 30 June 2006. In the undiverted reference streams, both the upper and lower reaches experienced natural flow. The diversion reduced August mean flow by 50–85% and the seven-day minimum flow by 66–97%. At all three diverted sites, the disturbed reach had a significantly lower minimum daily flow, seven-day minimum flow, and mean flow relative to the undisturbed reach (see Appendix A).

We used Mt. Hope River, a nearby stream gauged by the USGS since 1940, to put our values into a historical

context (USGS, NWIS database, *available online*).² We used May–September 2006 hydrological data for our undisturbed reaches and Mt. Hope River to determine if they were closely correlated. Using nonlinear regression we found we could predict discharge for our undisturbed reaches based on the Mt. Hope data as the relationship was well described by a power relationship, $y = ax^b$, for all three streams ($R^2 = 0.95$, $R^2 = 0.91$, and $R^2 = 0.96$). We used these relationships to estimate historical discharge and calculate low-flow indices for our streams. We found that the minimum daily flow at two of the disturbed reaches was lower than the Q_{99} value (the amount of discharge exceeded 99% of the time), and for the third site it was lower than the Q_{95} value (Gordon et al. 2004).

Stable isotope sampling

We used stable isotope techniques to estimate realized food chain length because they provide a robust, continuous measure of food chain length that integrates all pathways leading to the top predators (Vander Zanden et al. 1999, Post et al. 2000, Post 2002b). We collected organisms for isotopic analysis in both 100-m reaches for the six streams. The non-predatory stream insects used for isotopic baselines were collected at three time periods during the summer: 13–15 June, 18–21 July, and 22–24 August 2006. We collected potential top predators at the end of the summer. Predatory insects and crayfish were collected 22–24 August 2006 and fish were collected 1 and 5 September 2006. We collected insects and crayfish nonquantitatively using either a kicknet (insects) or small aquarium nets (crayfish). We used a BP-4 Coffelt backpack electro fishing unit (Coffelt Electronics, Englewood, Colorado, USA) to collect fish. In all cases, the whole organism was kept, placed on ice, and frozen. We collected representatives of all fish species, crayfish species, and predatory insect families. For fish, we found *Rhinichthys atratulus* (black-nosed dace), *Salvelinus fontinalis* (brook trout), *Lepomis cyanellus* (green sunfish), *Micropterus salmoides* (largemouth bass), *Catostomus commersonii* (white sucker), *Semotilus corporalis* (fallfish), *Notemigonus crysoleucas* (golden shiner), and *Lepomis gibbosus* (bluegill). We found one species of crayfish, *Cambarus robustus*. The most common predatory insects collected were Odonata (Aeshnidae), Megaloptera (Corydalidae), and Plecoptera (Perlidae). The nonpredatory insect families collected as potential baselines included Ephemeroptera (Heptageniidae), Plecoptera (Leuctridae, Peltoperlidae), and Trichoptera (Hydropsychidae, Philopotamidae).

Sample preparation and stable isotope measurements

We identified all samples for isotope analysis to species (fish, crayfish) or family (insects) and measured

² (<http://nwis.waterdata.usgs.gov/nwis/>)

their length. We then dried them at 60°C for 48 hours. For insects and fish the whole organism was dried, but for crayfish the soft tissue was removed from the shell and dried. For the smaller insects, individuals were pooled (2–20 individuals) for analysis, but larger insects, crayfish, and fish were run individually. We ground the samples to a fine powder using a mortar and pestle (insects and crayfish) or a SPEX Certiprep 6750 freezer mill (fish; SPEX Certiprep, Metuchen, New Jersey, USA). Isotope analysis was performed with a ThermoFinnigan DeltaPlus Advantage stable isotope mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA) at the Earth Systems Center for Stable Isotope Studies (ESCSIS) at the Yale Institute for Biospheric Studies. All stable isotope values were reported in the notation: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ([X_{\text{sample}}/X_{\text{standard}}] - 1) \times 1000$, where X is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The $\delta^{13}\text{C}$ values for all organisms were corrected for lipids using C:N ratios following Post et al. (2007). The standard deviation of replicates of ESCSIS animal standard (trout) within a tray of samples ranged from 0.02‰ to 0.14‰ for $\delta^{13}\text{C}$ and from 0.03‰ to 0.09‰ for $\delta^{15}\text{N}$.

Food chain length estimates

We estimated trophic position of predatory insects, crayfish, and fish using a two end-member mixing model following Post (2002b). We used a mean $\delta^{15}\text{N}$ enrichment of 3.4‰ to estimate trophic position (Post 2002b). The two end-members used for baseline calculations were mayflies from the family Heptageniidae (scrapers/collector-gatherers) and stoneflies of the family Peltoperlidae (shredders). Insect end-members were collected from each reach of every stream to calculate reach-specific $\delta^{15}\text{N}$ baselines. We used these two insect end-members because they integrate over the main basal food resources in the stream. The mayflies had $\delta^{13}\text{C}$ values in the range of -26‰ to -33‰ , which is representative of autochthonous inputs, while the stonefly $\delta^{13}\text{C}$ values ranged from -24‰ to -26‰ , which is representative of allochthonous inputs. In streams where the range of $\delta^{13}\text{C}$ values for the Heptageniidae was representative of the entire food web and few Peltoperlidae were present, a single baseline (Heptageniidae) was used. Food chain length was estimated as the trophic position of the apical predator, the predator that holds the maximum trophic position (Post et al. 2000, Post and Takimoto 2007).

Insect community composition

In addition to collection for isotope analyses, we carried out a quantitative assessment of insect community composition for each stream reach of our six streams. We used a WaterMark surber type stream bottom sampler (Aquatic Research Instruments, Hope, Idaho, USA), which we placed at three randomly selected riffle habitat locations and three randomly selected pool habitat locations within each 100-m stream

reach. At each location we disturbed all the substrate within a 0.3-m by 0.3-m area to dislodge the insects into the net. We placed each sample into a plastic bag with ethanol that we sorted within 24 hours. We identified insects to the genus level when possible (with the exception of dipterans, which we identified to the family level) using Merritt and Cummins (1996) and Peckarsky et al. (1990a). Insects were measured at 10 \times magnification to the nearest 0.5 mm.

Statistical analysis

All statistical analyses were performed in R (version 2.6.0; R Development Core Team 2006). To control for variation between streams we used difference data in our analyses. For example, in analyses of food chain length, values recorded for the lower reach (disturbed) were subtracted from food chain lengths measured in the upper reach (control). We used ANOVA to test for treatment effects (diverted vs. undiverted streams) on difference in food chain length. We used the same ANOVA design to determine if there were significant changes in insect family richness and in organism trophic position. We used data from the insect community composition surveys to assess insect family richness. We analyzed shifts in trophic position for a subset of organisms. Only fish, crayfish, and insect families that were abundant in both reaches of most of the streams were considered to ensure accurate trophic position estimates and an adequate sample size.

We used a Student's t test to look at organism size. For fish, we compared the differences (upper-lower reach) in average length of fish species in the diverted streams to the differences in the undiverted streams. For insects we used data from the community composition surveys and examined differences in average length of insect families. We used linear regression to examine relationships between organism size and trophic position. Relationships were examined at the species level for fish and crayfish and at the family level for insects.

RESULTS

Food chain length

Food chain length varied by over a full trophic position between streams, but within a stream the between-reach difference was slight, from 0.09 to 0.36 of a trophic position (Fig. 1). There was no significant effect of stream treatment (diverted vs. undiverted, ANOVA, $F_{1,4} = 3.95$, $P = 0.12$). The identity of the apical predator varied among streams, but was generally the same within a stream, with the exception of one undiverted stream. In all cases the maximum trophic position was held by a fish, either the black-nosed dace, green sunfish, largemouth bass, or white sucker.

Species loss

There was no loss of fish and crayfish species as a result of our low-flow disturbance; fish and crayfish species that were present in the undisturbed reach of a

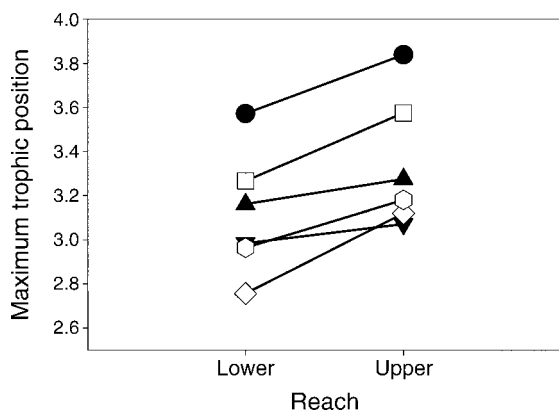


FIG. 1. Food chain length in upper and lower reaches of diverted (solid shapes) and undiverted (open shapes) streams. Diverted sites are outlet to Paine Pond (circle), Lead Mine Brook East branch (triangle), and Lead Mine Brook West branch (upside-down triangle). Undiverted sites are Bush Meadow Brook (square), outlet to Morse Reservoir (hexagon), and inlet to Morse Reservoir (diamond). All study sites are in Yale Myers Forest, Connecticut, USA.

diverted stream were also present in the disturbed reach. There was also no significant change in insect family richness with stream treatment (ANOVA, $F_{1,4} = 0.04$, $P = 0.85$; see Appendix B for richness values). There was some variability in the presence and absence of insect families, especially for rare families, but the loss and gain was generally idiosyncratic.

Trophic position

There was a considerable range in the average trophic positions of fish (2.7–3.8), crayfish (2.1–2.9), predatory insects (2.0–3.2), and nonpredatory insects (1.3–2.7) between streams, but there was no evidence of significant shifts in the trophic position of any group as a result of water diversion (see Appendix C: Table C1 for ANOVA results).

Body length

There were shifts in fish body length as a result of water diversion. In diverted streams, the fish in the undisturbed upper reach were larger than those in the disturbed lower reach while in undiverted streams there was little size difference between upper and lower reaches (Fig. 2a, Student's t test, one-tailed, $P = 0.05$). In disturbed reaches, the larger fish showed a 30% to 40% decrease in body length while smaller fish showed a 10% decrease in body length (Fig. 2b). This indicates that larger fish species were more sensitive to the effect of our low-flow disturbance than smaller fish. We found no significant effect of our low-flow disturbance on the difference in average body length of insect families (Student's t test, one-tailed, $P = 0.10$).

There was no significant relationship between body length and trophic position for most species of fish (green sunfish, $R^2 = 0.002$, $F_{1,13} = 0.02$, $P = 0.88$; black-nosed dace, $R^2 = 0.03$, $F_{1,54} = 1.47$, $P = 0.23$; largemouth

bass, $R^2 = 0.06$, $F_{1,8} = 0.50$, $P = 0.50$; Fig. 3). Brook trout did show a slight increase in trophic position with length, but were not the apical predator in any stream ($R^2 = 0.36$, $F_{1,9} = 5.01$, $P = 0.05$; Fig. 3). Crayfish showed a decrease in trophic position with length ($R^2 = 0.22$, $F_{1,40} = 11.25$, $P = 0.002$), as did dragonfly larvae (Aeshnidae) ($R^2 = 0.42$, $F_{1,10} = 7.12$, $P = 0.02$; Fig. 3). There was no significant relationship between trophic position and body length for other families of predatory insects or nonpredatory insects (Fig. 3; Appendix C: Table C2).

DISCUSSION

Streams are an ideal system to test for the effect of disturbance on food chain length because they are subject to natural hydrological variation, and hydrolog-

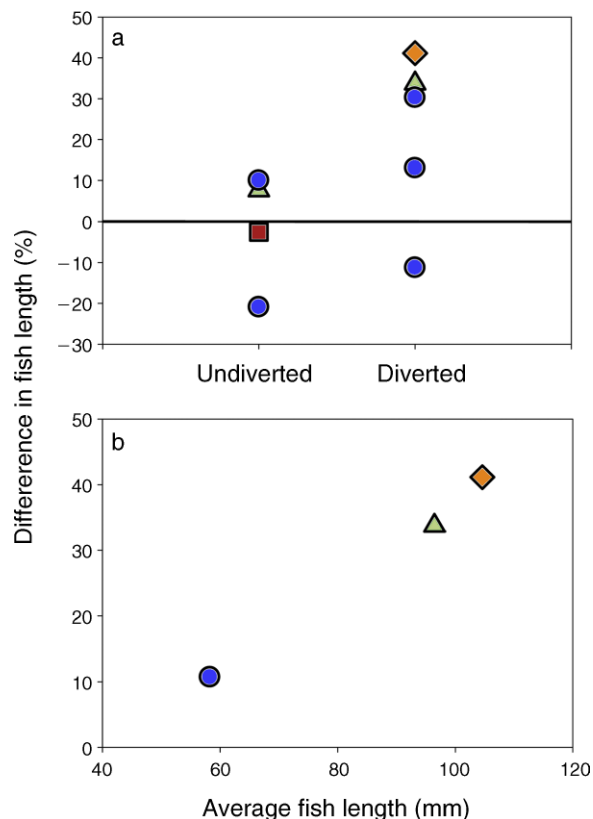


FIG. 2. (a) Percentage difference in the length of fish species (between upper and lower reaches) for undiverted and diverted streams. Percentage difference in fish length is calculated for each fish species in each stream in which it was present. It is the difference in fish length (average length in upper reach – average length in lower reach) divided by the average length of fish in the upper reach. Fish are largemouth bass (square), green sunfish (triangles), brook trout (diamond), and black-nosed dace (circles). The line marks where there is no difference in fish size between the upper and the lower reach. (b) The percentage difference in fish length for diverted streams, or the average difference if the fish was present in multiple streams, plotted against the average length of that fish species (calculated from individuals in undisturbed reaches). Fish symbols are the same as in (a).

ical regime is a dominant force structuring communities (Resh et al. 1988). They are also an important system in which to understand the role of disturbance. Dam construction and the diversion of water for consumptive use have substantially altered the natural hydrology of streams, and climate change is likely to further affect hydrological regimes and the frequency of extreme events such as droughts and floods (Arnell et al. 1996). We did not find an effect of an experimental low-flow disturbance on realized food chain length. This finding suggests that disturbance is not a key factor determining food chain length in our streams and supports previous studies that have suggested that food chain length is an insensitive indicator of disturbance compared to changes in general community structure (Jenkins et al. 1992, Townsend et al. 1998).

Disturbance may differentially affect organisms based on their behavior, size, and life-history characteristics (Power et al. 1996). This effect may be direct or mediated through shifts in habitat or resource availability. In this study, the greatest effect of our experimental low-flow disturbance was on the largest organisms. By the end of the summer, the largest fish found in our streams were not present in the disturbed reach even when abundant in the undisturbed reach of the same stream. Large fish require a greater habitat volume than small fish and invertebrates, and our experimental disturbance reduced water volumes by 37% to 56% relative to undisturbed reaches. Our results support previous work in streams that saw a decreased abundance of fish predators under drought conditions (Power et al. 1995, Marks et al. 2000), and suggests that this effect may be due to changes in habitat availability.

Fish were not lost completely from the disturbed reach due to the highly heterogeneous nature of stream systems (Palmer and Poff 1997). The low-flow disturbance caused areas of the streams to dry completely but, due to the geomorphology of our streams, there were still isolated deeper pools present. It was in these pools that the fish became concentrated and were able to survive, albeit at a smaller size (A. Walters, *personal observation*). We infer from this pattern that the presence of refugia in streams may make local extinctions rare and allow dynamical constraints to operate weakly, if at all (Thompson and Townsend 2005).

The expectation that disturbance should reduce food chain length derives in part from the assumption that predators are typically larger than their prey (Cohen et al. 1993), that trophic position typically increases with body size (France et al. 1998, Jennings et al. 2001), and that the largest organisms are most susceptible to disturbance (Pimm and Kitching 1987). Under these assumptions, disturbance should shorten food chain length. In our streams, disturbance did remove the largest individuals, but because body size was not strongly related to trophic position, there was no commensurate decrease in food chain length. Trophic

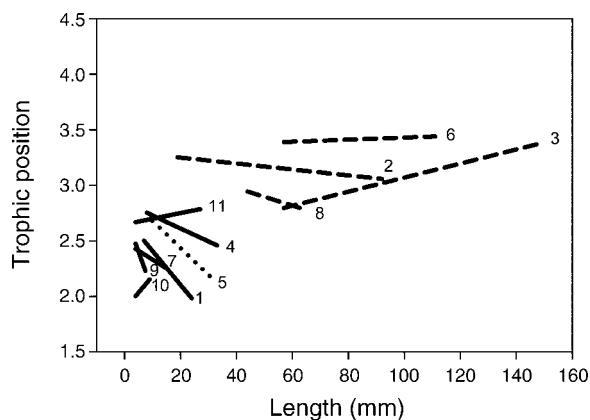


FIG. 3. Linear regression lines of trophic position against length for a taxonomic group. Each regression is derived from individual estimates of trophic position plotted against individual estimates of length (mm). Dashed lines represent fish species, dotted lines represent crayfish species, and solid lines represent insect families. Organisms are (1) Aeshnidae, (2) black-nosed dace, (3) brook trout, (4) Corydalidae, (5) crayfish, (6) green sunfish, (7) Hydropsychidae, (8) largemouth bass, (9) Leuctridae, (10) Philopotamidae, and (11) Perlidae (see Appendix C: Table C2 for linear regression statistics).

position did not increase with fish size because the fish are too small to be piscivorous and mostly feed on insects. When aggregated at the family level, insects hold basically the same trophic position irrespective of size. Thus, as fish get larger, they are not feeding at a higher trophic position, even though they may be eating larger prey. The assumed relationship between body size and trophic position is often not met in diverse food webs in which consumer body sizes are highly variable (Layman et al. 2005).

The dynamical constraints hypothesis is more likely to hold in simple systems that conform to the original assumptions of the models. Previous studies demonstrating an effect of disturbance on food chain length have mostly worked with small food webs on a small spatial scale (Pimm and Kitching 1987, Jenkins et al. 1992, Lawler and Morin 1993). These simple food webs typically meet the assumptions and correspond closely to the linear food chains modeled by the dynamical constraints hypothesis (Pimm and Lawton 1977, Pimm 1982).

Hydrological disturbance in streams encompasses both high-flow and low-flow events. Despite increasing recognition of the importance of low-flow disturbance in streams (Lake 2000, Riseng et al. 2004, Sabo and Post 2008), low-flow events are still poorly studied and previous research on food chain length and disturbance in streams has focused on flood disturbance (Townsend et al. 1998, Marks et al. 2000, Parker and Huryn 2006). Floods may have a larger effect on food chain length as they cause greater immediate mortality. Results from our low-flow disturbance suggest that droughts do not reduce food chain length unless complete desiccation eliminates fish and predatory insects. However, com-

pletely dry streambeds are unrealistic for perennial streams in this region; therefore our low-flow disturbance constituted a considerable and realistic disturbance in which minimum daily flow declined by 58–98% in disturbed reaches. At the Paine Pond location, this minimum daily flow value corresponded to an event with a 60-year reoccurrence interval, whereas the reoccurrence interval was <10 years at the other two sites. Despite this spatial variation, there was no difference in the response of food chain length, and we conclude that even a very intense low-flow event did not alter food chain length.

The loss of larger fish from our disturbed stream reaches could have altered the strength of species interactions in our streams. Some previous studies use a functional measure of food chain length (Marks et al. 2000) that considers only strongly interacting species (Power et al. 1996). In contrast, we measured realized food chain length using stable isotopes because it provided a reliable estimate of food web structure that is closer to those used in theoretical models (Pimm 1982, Sterner et al. 1997). The shift in fish size structure in our streams may have altered functional food chain length, but the structural complexity of the food web allowed compensation and resulted in no change in realized food chain length.

Disturbance, and in particular the dynamical constraints hypothesis, has been viewed for over 30 years as an important mechanism regulating variation in food chain length. Effects of disturbance were thought to be especially relevant for ecological systems that experience high levels of temporal variation, such as streams, temporary ponds, and intertidal habitats. Our ecosystem-scale manipulation provides a robust experimental demonstration that a low-flow disturbance does not affect food chain length in streams. Although more research is required to identify the precise reason for this pattern, we suggest that the lack of a disturbance effect is due to habitat refuges and a complex food web that does not conform to the assumptions of models originally used to develop theoretical predictions.

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APPENDIX A

Hydrological indices for the disturbed and undisturbed reach for the three diverted streams (*Ecological Archives* E089-187-A1).

APPENDIX B

Community richness values for all stream sites (*Ecological Archives* E089-187-A2).

APPENDIX C

Trophic position statistics (*Ecological Archives* E089-187-A3).