

Shoaling species drive fish assemblage response to sequential large floods in a small midwestern U.S.A. stream

Jeff Scott Wesner

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Abstract I assessed the short-term impact of two sequential scouring floods on the fish assemblage of a small prairie stream. I tested for changes in fish abundance, fish assemblage composition, and fish-habitat associations within individual pools and across a suite of pools following each flood. Before the second flood, 30–90% of fish were removed by seining in five of eight pools. Overall fish abundance was reduced by approximately 50% following the first flood, but effects varied widely among individual pools. Fish abundance was unaffected by the second flood, despite prior removal of a known proportion of fish, suggesting recolonization of defaunated pools during the flood. Fish assemblage similarity across the entire suite of pools was low following each flood, but varied considerably within individual pools. Defaunated pools were more similar to pre-flood assemblages than control pools, though the mechanism behind this pattern was unclear. Changes in abundance and assemblage composition were driven

by interpool movement of two minnow species with the shared behavioral trait of shoaling: bigeye shiner *Notropis boops* and central stoneroller *Campostoma anomalum*. Shifts in abundance showed no upstream or downstream pattern, suggesting that flooding allowed fish to move actively among pools that are typically isolated by partial barriers (riffles). This study highlights the importance of considering species' behavioral traits when assessing the impacts of flooding, and suggests that shoaling behavior may be useful trait for predicting fish assemblage change following flooding.

Keywords Flood · Fish assemblages · Shoaling · Minnow · *Notropis* · *Campostoma*

Introduction

The structure of stream fish assemblages is an important factor determining ecosystem function in streams (Hargrave 2006). Even small changes within an assemblage, such as fish species identity in the same trophic group, can have large consequences for stream and riparian ecosystems (Baxter et al. 2004). It is therefore important to understand how disturbance in streams affects fish assemblage structure, especially in light of global climate change, which is predicted to alter both the frequency and magnitude of disturbances such as floods and drought in streams (Poff et al. 1996).

J. S. Wesner (✉)
Department of Zoology and Biological Station,
University of Oklahoma,
Norman, OK 73019, USA
e-mail: jeffwesner@gmail.com

Present Address:
J. S. Wesner
Department of Biology, Brigham Young University,
401 WIDB,
Provo, UT 84602, USA

The immediate impact of floods on fish assemblages varies according to the magnitude and timing of the flood (Matthews 1998), the resilience of fishes to disturbance (Dodds et al. 2004), and the scale of the study. Studies of flood effects on fishes often focus on changes within an entire reach, encompassing several distinct microhabitats (pools/riffles/runs) (e.g. Meffe and Minckley 1987; Franssen et al. 2006). At this scale, flood effects on fish assemblages vary from negligible (Moyle and Vondracek 1985; Meffe and Minckley 1987; Lobòn-Cervià 1996) to large (Harrell 1978; Matthews 1986). Less studied are flood effects within microhabitats along a stream reach, such as pools isolated by riffles (Matthews et al. 1994). Fish assemblage structure at this scale may be more biologically meaningful, because biotic interactions are more likely within isolated pools than within an entire reach (Matthews and Marsh-Matthews 2006). For example, Matthews et al. (1994) showed that pools with large numbers of predatory fish had low numbers of prey fish before floods, but following large floods, some ‘predator’ pools contained large numbers of prey fish. Because pools are often partially isolated by barriers such as riffles (Lonzarich et al. 2000; Schaefer 2001), such small-scale changes may have long-term consequences for stream fish that become decimated by predation following the return of the stream to base flow, but these patterns would be missed in studies limited to reach-scale dynamics of fish assemblages, as opposed to more discrete habitats, like individual pools.

Prairie headwater streams are characterized by a harsh flow-regime involving periods of extended drought followed by short, but sometimes drastic floods (Power and Stewart 1987; Dodds et al. 2004). Harsh environmental regimes act as a selection factor for fishes, resulting in fish assemblages composed of species that are often resistant and/or resilient to floods (Dodds et al. 2004). Thus, floods are unlikely to alter fish assemblages in the long-term when species exhibit adaptation to environmental disturbances (Poff and Allan 1995). However, variation in species traits within a local fish assemblage may drive differences in assemblage structure within microhabitats (pools) in the short-term. Most studies census post-flood fish assemblages at the reach scale several weeks, months or years after the flood recedes (Harrell 1978; Meffe and Minckley 1987; Pearsons et al. 1992; Pires et al. 2008). In cases

where fish assemblages are found to be stable, such intervals after a flood make it unclear whether similarity is due to resilience of fishes following disturbance or due simply to a lack of flood effect.

Scouring floods can alter fish assemblages indirectly by disturbing fish habitat through exposing bedrock, washing out sand, uprooting riparian trees, and rearranging the riffle-pool structure in streams, though specific effects may vary drastically from pool to pool (Matthews 1986). In lotic systems, habitat structure can be a primary determinant of organism distribution and abundance, but habitat is itself a product of stream flow regimes and can be altered substantially during floods (Poff and Ward 1990). Fish are commonly associated with instream habitat (Matthews 1998), but flooding may disrupt fish-habitat associations. In streams where fish assemblages are associated with both biotic and abiotic conditions, floods may alter assemblage composition only within habitats where abiotic variables are strongly altered by a flood, interrupting fish-habitat associations (Matthews 1998). For example, Matthews (1998, p. 330) noted that pools with large bass were filled in with gravel following a large flood in the Baron Fork River, OK, USA, forcing movement of bass out of these habitats.

The goal of this study was to examine how fish assemblages in individual pools and across an entire suite of pools changed immediately following two sequential large floods in a small, prairie-margin stream. The following specific questions were addressed: 1) Does flooding alter the distribution, abundance, and assemblage structure of fishes within and among whole stream pools? 2) Are responses of individual species dependent on fish shoaling behavior? 3) Are shifts in assemblage structure deterministic or random with respect to stream habitat?

Methods

Study site

Brier Creek is a clear, small tributary of the Red River arm of Lake Texoma in Marshall County, Oklahoma, USA. Sampling occurred in May, June, and July 2007 across seven to nine pools along a 1-km reach described in detail by Power and Matthews (1983) (Fig. 1). At this site the stream maintains permanent

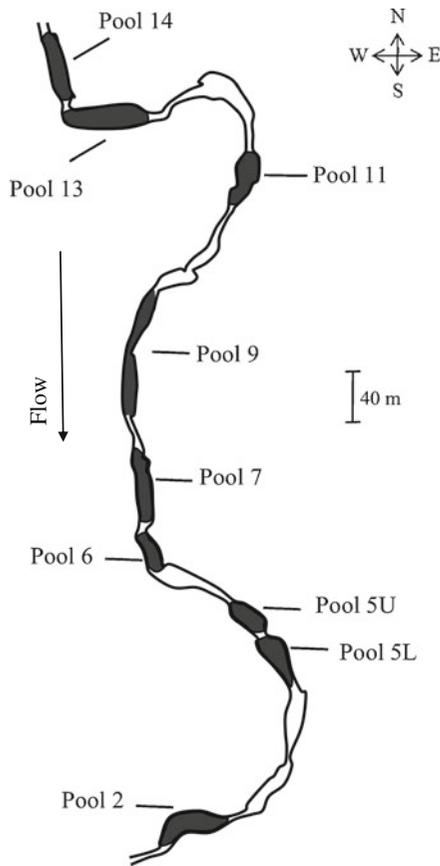


Fig. 1 Map of study pools in Brier Creek, OK, USA

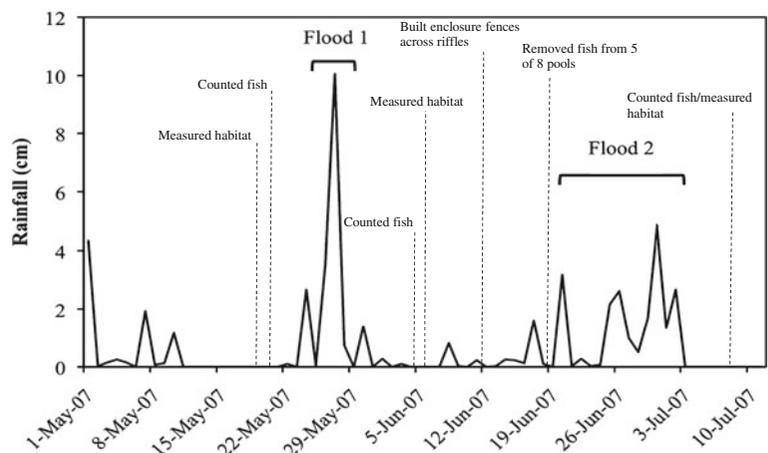
flow in a pool-riffle pattern in all but the driest years. Pool numbering in my study followed that of Power and Matthews (1983), except that I considered their pool 5 to be two distinct pools before and after the

second flood, with an upper and lower division (pools 5U and 5L, respectively). Additionally, I surveyed their pool 6 only in the upper reach on all dates. During base flow, the pools selected for this study varied from 20–80 m long, 15–45 cm mean depth, and 5–10 m mean width. Pools with a maximum depth exceeding 1 m were present in the reach, but were not sampled due to low visibility and the need to select pools from which fish could be thoroughly seined upon removal. Water temperature was relatively constant (range: 25–27°C), and canopy cover varied from 0–70% among pools.

Floods

Two large, physically turbulent floods occurred in May and June 2007 (Fig. 2), during the rainiest spring on record for Oklahoma (Oklahoma Climatological Survey, Norman, OK), each of which caused major scour of the reach. Brier Creek is not gauged, but there is a good correspondence between major rainfall events and stage rises in this stream (Power and Stewart 1987; Matthews and Marsh-Matthews 2006). The first flood began on 27 May, when 13.5 cm of rain fell over 48 h, as recorded by a weather monitoring station located 15 km from the study site (Fig. 2). On 28 May I recorded a stage rise of 2.5 m on Brier Creek, estimated from debris lines and watermarks on trees. Only twice has a stage rise exceeding this level been recorded in Brier Creek since 1983 (Matthews and Marsh-Matthews 2006). The flood receded rapidly, reaching near base flow by 1 June, though clarity remained low until 5 June.

Fig. 2 Rainfall and sampling timeline. Rainfall was recorded from a permanent weather station located 15 km from the study site



The second flood began on 20 June, and was marked by three large 24-h rain events (Fig. 2), which prevented the stream from reaching normal flow until 3 July, 13 days after the initial stage rise. During this period of prolonged flooding I recorded a maximum stage rise of 1 m on 30 June based on debris estimates, with flow velocity reaching at least 1.1 m/s as measured from a downstream bridge on 28 June, nearly 50 times greater than normal base velocity (0.02 m/s).

Fish census

I documented fish assemblages by snorkeling whole pools on 21 May (6 days before flood 1), 5 June (4 days after flood 1 receded and 15 days before flood 2), and 8 July (5 days after flood 2 receded; see Fig. 2 for sampling timeline). Snorkeling is an effective method in small clear streams and has been used in surveys in Brier Creek for several decades (Matthews et al. 1994; Matthews and Marsh-Matthews 2006). All surveys occurred in midmorning on sunny days when visibility in all pools was high. I snorkeled seven pools on 21 May, 10 on 5 June, and 8 on 8 July. Pool numbering differed slightly between sample dates to accommodate the setup of a separate experiment, though the June survey included pools common to both May and July surveys (Appendix 1). For this reason I compared data before and after a given flood only for pools that were common to consecutive sample dates (i.e. May vs. June and June vs. July). On each date I snorkeled from downstream to upstream in a zig-zag pattern, enumerating fish abundance in an entire pool following techniques in Power and Matthews (1983). Fish were identified to species, except for bass *Micropterus* spp., which contain two species (largemouth *M. salmoides* and spotted bass *M. punctulatus*) that are difficult to distinguish by snorkeling (Matthews et al. 1994). Orangefthroat darters *Etheostoma spectabile* were excluded from analyses due to the difficulty of obtaining accurate snorkel counts of this species, which hides in the benthos under rocks (Matthews et al. 1994). Plastic mesh fencing (5 mm) was erected across the entire stream channel at the upstream and downstream end of ten pools on 12 June to restrict among-pool movement of all but the smallest young-of-year fish. On 19 June, after the first flood, 30–90% of fish were removed from five pools by seining and placed in the nearest non-experimental upstream or downstream pool (50–100 m from experimental pools; removal estimates based on 5

June snorkel survey). Seining was limited to two to three pool-long hauls with care made to minimize substrate disturbance. The other five pools were seined to mimic substrate disturbance, but no fish were removed. One day after fish removal (20 June) the second flood destroyed the fencing, meaning that fish were not restricted to pools during or after the flood. I resurveyed eight of the ten pools (five defaunated pools and three control pools) on 8 July to measure recolonization.

Habitat

Pool size (mean depth and width) and substrate type were recorded in individual pools on 20 May, 6 June, and 8 July (Fig. 2). To measure depth and substrate type, three to four equally spaced transects were placed across each pool, and depth and dominant substrate type were measured at 1 m intervals along each transect (per Power and Matthews 1983). Substrate was classified as sand (<2 mm) gravel, (2–10 mm) pebble (10–30 mm), or bedrock following Gorman and Karr (1978), and measured as percent of each substrate type in each pool. The width of each transect was averaged to obtain a mean width for each pool.

Fish data analysis

Mean fish abundance was compared between sample dates using a paired *t*-test. Pools were replicates for reach comparisons, and species were replicates for individual pool comparisons. Data were log transformed and tested for normality using the Shapiro-Wilk test. For non-normal data a Wilcoxon rank-sum test compared pre- and post-flood fish abundance. Fish assemblage structure was assessed using several approaches. First, the rank abundance of each species was compared among pools using Spearman's rank correlation (Grossman et al. 1982). A significant correlation would indicate that rank abundance of individual species did not change following a flood. Second, the Morisita-Horn (C_{MH}) index of similarity was used to measure the similarity of fish assemblages before and after a flood within individual pools. This index indicates similarity on a scale of 0 (completely different) to 1 (exactly the same), which allows a more quantitative measure of fish assemblage structure and allows comparison with other studies (sensu Meffe and Sheldon 1990). Values between 0.0 and 0.5 were classified as "low" similarity

and values greater than 0.75 as ‘high,’ following Matthews et al. (1994), though it should be emphasized that any such cut-off is subjective. Values between 0.51 and 0.74 were considered generally similar, but were given no special emphasis. Third, a Bray-Curtis dissimilarity matrix was created based on the abundance of each species in each pool on each date. Matrices before and after each flood were compared for concordance of matrix patterns using a Mantel test with 10,000 random permutations. Lastly, a correspondence analysis (CA) was performed on each dataset (May, June, and July snorkel data). The scores on the first two CA axes of pre- and post-flood datasets were used as input matrices in a Procrustean superimposition, which graphically compares the relationship between multivariate datasets using residual vectors (Peres-Neto and Jackson 2001; PROCPLLOT, NTSYSpc 2.11).

Habitat data analysis

Mean habitat data were compared between each consecutive sample date using a paired *t*-test on natural log or arcsine square root (proportions) transformed data, using each pool as a replicate. Non-normal data were compared using a Wilcoxon rank-sum test.

Fish habitat associations

I tested for correlations between individual pool habitat and fish assemblage structure by comparing a habitat and fish matrix using a Mantel test with 10,000 random permutations. Habitat similarity matrices were based on Euclidean distance and fish similarity matrices were based on the Morisita-Horn index as suggested by Diniz-Filho and Bini (1996). Acceptance of the null hypothesis of no association of these matrices would indicate that species assemblages in pools with similar habitat conditions did not differ from assemblages in pools with different habitat conditions (Taylor et al. 1993).

Results

Flood 1

Fish

Five pools showed strong declines in fish abundance (40–92%), while two pools showed strong increases

(183% and 357%; Table 1). Because of this variation among pools in the magnitude and direction of change, a *t*-test comparison of pre-/post-flood fish abundance using pools as replicates was not significant ($t_6=0.979$, $p=0.365$), despite an overall reduction in total fish abundance by nearly 50% (Table 1). Species richness was higher after the first flood ($n=7$) than before the flood ($n=5$) due to the appearance of blackstripe topminnows *Fundulus notatus*, orangespotted sunfish *Lepomis humilus*, and central stonerollers *C. anomalum*, and the loss of green sunfish *Lepomis cyanellus* in post flood surveys.

Assemblage structure differed after the first flood. Rank abundance of fish species in the suite of pools was not correlated between sample dates ($p>0.05$, Table 1), and only a single pool had significantly correlated rank abundance (Pool 6, $p=0.02$, Table 1). Most of the change occurred as a result of a switch in abundance of the dominant species. Bigeye shiners averaged 81% of total abundance before the flood, but only 27% after ($t_6=2.736$, $p=0.034$; Table 2; Fig. 3). Central stonerollers were absent in pre-flood samples, but abundant post-flood ($n=260$), though 83% of stonerollers were observed within a single pool which contained 217 individuals after the flood, resulting in a significant increase in post-flood abundance of this species (Wilcoxon $z=-2.028$, $df=1$, $p=0.043$; Table 2; Fig. 3). Despite changes in rank abundance, assemblage composition based on the Morisita-Horn index of similarity was above 0.5 for 5/7 pools, though only two pools were above the 0.75 threshold of ‘high’ similarity. For the pools with the lowest percent similarity (0.23 and 0.17), scores reflect either the post-flood appearance of a large school of central stonerollers or the disappearance of a large school of bigeye shiners. A Mantel test comparing Bray-Curtis dissimilarity matrices showed no correlation between pre- and post-flood fish assemblages among pools (normalized Mantel $Z=-0.145$, $p=0.196$), suggesting a restructuring of the fish assemblage at the reach scale.

The first two CA axes accounted for 77% and 68% of total variation for May and June datasets, respectively. Procrustes superimposition showed substantial movement of individual pools in multivariate space (Fig. 4a).

Habitat

Habitat structure in the entire reach was similar pre- and post-flood, though several pools were altered substantial-

Table 1 Total fish abundance in each pool, Morisita-Horn index of similarity (C_{MH}), and Spearman's Rho (rank correlation) for each pool and averaged across all pools (mean and standard error (SE)). Bolded values for Spearman's Rho

indicate a correlation of species ranks significant at $\alpha=0.05$. Treatment indicates whether fish were removed from an individual pool between sample dates, – fish removed, + fish not removed

Total abundance						
Flood 1	Pool	21 May	5 June	C_{MH}	Spearman's Rho	Treatment
	2	350	49	0.65	0.62	+
	5	105	63	0.97	0.66	+
	6	159	12	0.89	0.79	+
	9	107	303	0.23	0.53	+
	11	21	96	0.68	0.29	+
	13	118	30	0.17	0.03	+
	14	121	11	0.56	0.59	+
	Mean	140	81	0.59	0.50	
	SE	38	39	0.11	0.10	
Flood 2	Pool	5 June	8 July	C_{MH}	Spearman's Rho	Treatment
	5L	4	1	0.67	1.00	–
	5 U	59	146	0.68	1.00	–
	6	12	9	0.01	–0.45	+
	7	4	32	0.00	–0.21	–
	9	303	72	0.11	0.08	+
	11	96	58	0.44	0.51	–
	13	30	19	0.57	0.60	–
	14	11	64	0.10	0.05	+
	Mean	65	50	0.32	0.32	
	SE	34	16	0.10	0.18	

ly. In 66% of pools, bedrock was more abundant after the flood (Table 3). In the two most downstream pools (2 and 5), sand was prevalent before the flood, but washed out or reduced after the flood, exposing bedrock (Table 3). In pool 2, washed out sand exposed an approximately 0.5 m deep bedrock shelf.

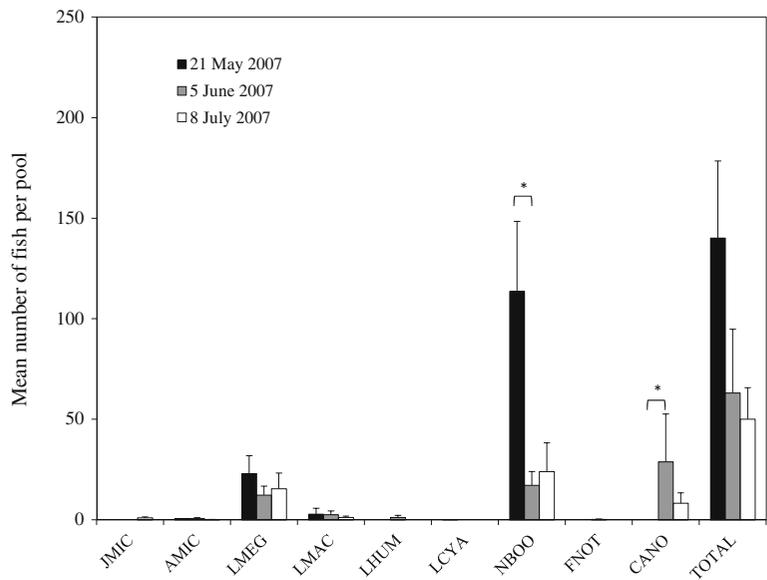
Fish habitat associations

Mantel tests showed no correlation between fish and habitat similarity matrices on either date (May: normalized Mantel $Z=-0.141$, $p=0.2612$; June: $Z=-0.058$, $p=0.4120$), suggesting that the measured

Table 2 Relative abundance of fish species in Brier Creek on each snorkel date during 2007

Species	Common name	21-May	5-Jun	8-Jul
<i>N. boops</i>	Bigeye shiner	0.81	0.26	0.48
<i>L. megalotis</i>	Longear sunfish	0.16	0.21	0.31
<i>L. macrochirus</i>	Bluegill	0.02	0.01	0.02
<i>Micropterus spp.</i> (adult)	Bass	< 0.00	< 0.01	< 0.01
<i>L. cyanellus</i>	Green sunfish	< 0.01	0.00	0.00
<i>Micropterus spp.</i> (juvenile)	Bass	0.00	0.00	0.02
<i>L. humilus</i>	Orangespotted sunfish	0.00	0.02	0.00
<i>F. notatus</i>	Blackstripe topminnow	0.00	0.00	0.00
<i>C. anomalum</i>	Central stoneroller	0.00	0.48	0.16

Fig. 3 Mean and standard error of fish abundance averaged across all pools. JMIC = juvenile *Micropterus spp* (<100 mm), AMIC = adult *Micropterus spp.* (>100 mm), LMEG = *Lepomis megalotis*, LMAC = *Lepomis macrochirus*, LHUM = *Lepomis humilis*, NBOO = *Notropis boops*, FNOT = *Fundulus notatus*, CANO = *Campostoma anomalum*, LCYA = *Lepomis cyanellus*. Significant differences ($p < 0.05$) between sample dates are indicated by an asterisk



pool characteristics did not contribute to fish assemblage structure.

Flood 2

Fish

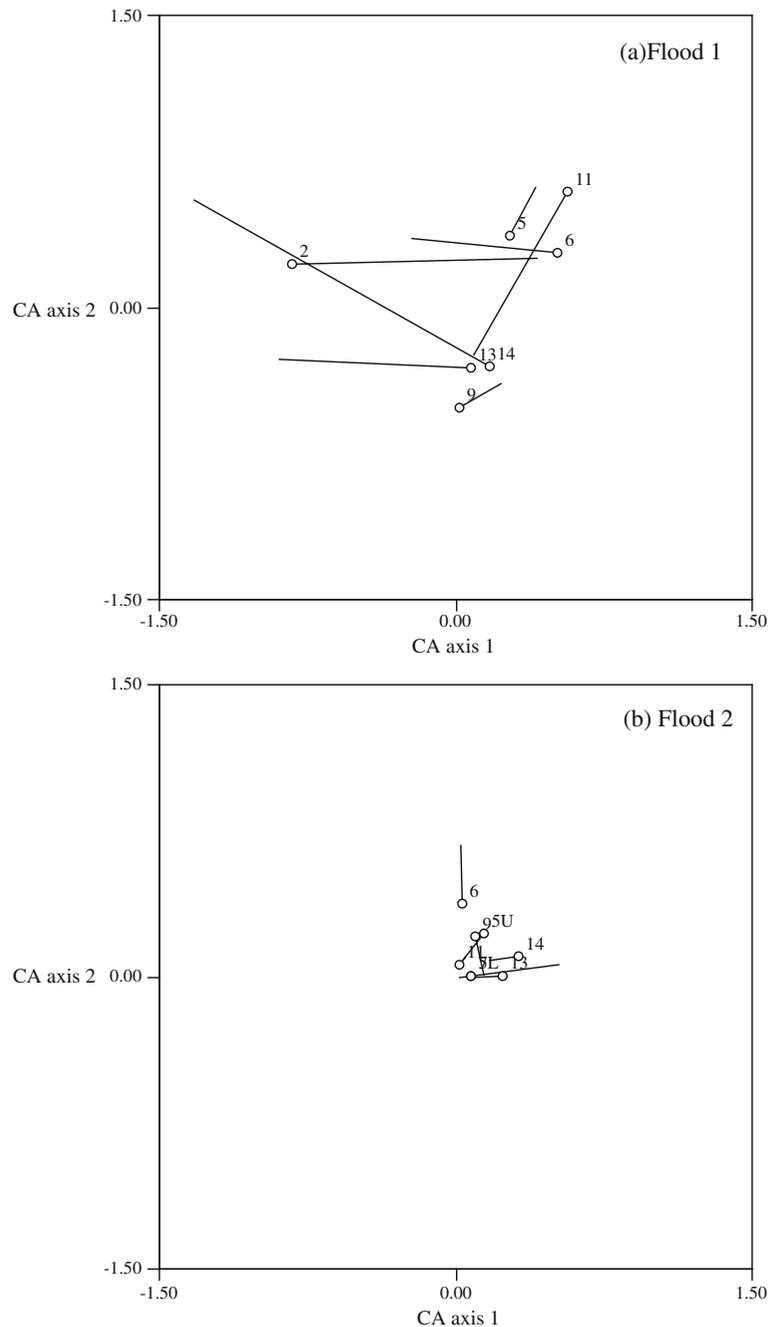
Fish abundance among pools and individual species abundance was similar following the second flood (among pools: $t_7=0.435$, $p=0.677$; each species: $p \geq 0.05$), despite the removal of at least 30% of all fish from five of the eight pools prior to the flood. The magnitude and direction of change varied among pools, with five pools showing sharp declines in fish abundance (25–76%), and three pools showing sharp increases (147–700%). Similarity in most pools was low following the flood. Fish assemblages in defaunated pools were more similar on average to pre-flood assemblages after the flood than control pools, based on the Morisita-Horn index (0.47 vs. 0.09, respectively; $t_3=2.351$, $p=0.06$). In other words, the flood resulted in the repopulation of fish removal pools with assemblages more similar to that of pre-flood assemblages than in control pools, which had almost entirely different assemblages after the flood.

Rank abundance for the suite of pools was not correlated between June and July ($r_s=0.639$, $p=0.088$).

Change in species ranks was largely restricted to upstream pools. The largest shift in species rank occurred between bigeye shiners and central stone-rollers, which were the most abundant species in the reach, and changes to rank abundance in most pools reflected a switch in the order of these two species. A t -test of mean rank correlation (Spearman’s Rho) between fish removal pools and control pools was not significant ($t_3=0.168$, $p=0.872$), suggesting that fish removal had no greater effect on post-flood rank abundance than the flood itself, though it should be noted that replication of the control pools was low ($n=3$), likely limiting the power of the t -test. Bray-Curtis dissimilarity matrices for all pools on 5 June and 8 July 2007 were not correlated (normalized Mantel $Z=0.107$, $p=0.7211$) suggesting that average assemblage structure in a given pool on 5 June was different on 8 July.

The first two CA axes accounted for 66% and 70% of total variation for June and July datasets, respectively. The movement of individual pools in multivariate space using Procrustes superimposition appeared lower than movement of a similar suite of pools in the first flood based on Procrustes residual vectors (Fig. 4b), suggesting the magnitude of change to the fish community following the second flood was less drastic than the after first flood.

Fig. 4 Procrustes superimposition of individual pools based on the first two axes of a correspondence analysis using \log_{10} -transformed fish snorkel data for each census date. Pools are labeled next to their pre-flood coordinates (*circles*). *Solid lines* indicate Procrustes residual vectors, with the endpoint of each line marking the position of post-flood coordinates. **a** Flood 1—May (*circles*) and June (*line end points*). **b** Flood 2—June (*circles*) and July (*line end points*)



Habitat

Habitat variables across the suite of pools were not significantly different between sample dates. Bedrock and rubble were the dominant substrate types in each pool on both sample dates, comprising between 77% and 100% of the substrate in each pool. Sand/silt was absent in June, but present in half of the pools in July,

though in small amounts (Table 3). This is in contrast to flood one, in which post-flood pools contained less sand/silt on average. This difference may be due to the difference in duration and magnitude between floods one and two. Flood two lasted twice as long as flood one, due to continued rain and increased soil saturation, but resulted in less than half the measured stage rise of flood one. Flood two also appeared to

Table 3 Pre- and post-flood habitat characteristics for each pool on each date. Pool number for 6 June differed to accommodate the setup of a separate experiment. Pool 5 was split into two sections for the analysis of flood 2, due to the

appearance of a riffle between the upper (U) and lower (L) sections. Data from 6 June for flood 1 represent the mean of these two sections of pool 5

Pool	Mean depth (cm)	Mean width (m)	Substrate (proportion)				Mean depth (cm)	Mean width (m)	Substrate (proportion)			
			Sand	Gravel	Rubble	Bedrock			Sand	Gravel	Rubble	Bedrock
Flood 1 21 May							6 June					
2	24.6	5.63	0.46	0.35	0.00	0.19	15.8	8.73	0.15	0.00	0.32	0.53
5	29.3	6.58	0.17	0.41	0.11	0.31	36.6	8.85	0.00	0.13	0.54	0.33
6	26.2	6.05	0.00	0.58	0.00	0.42	19.5	8.10	0.00	0.00	0.34	0.66
9	19.2	6.00	0.00	0.85	0.00	0.15	24.8	5.10	0.00	0.05	0.38	0.57
11	27.2	9.42	0.00	0.55	0.00	0.45	24.0	5.63	0.00	0.00	0.60	0.40
13	25.9	7.01	0.00	0.31	0.00	0.69	24.8	5.10	0.00	0.05	0.38	0.57
14	17.6	8.68	0.03	0.78	0.00	0.19	27.7	8.03	0.00	0.23	0.33	0.43
Flood 2 6 June							8 July					
5L	45.2	10.08	0.00	0.11	0.51	0.38	43.1	9.95	0.13	0.00	0.53	0.35
5U	28.0	7.63	0.00	0.14	0.57	0.29	37.4	6.08	0.06	0.06	0.41	0.47
6	19.6	8.10	0.00	0.00	0.34	0.66	21.0	8.29	0.00	0.00	0.48	0.52
7	24.0	5.63	0.00	0.00	0.60	0.40	33.0	8.77	0.00	0.00	0.75	0.25
9	24.9	5.10	0.00	0.05	0.38	0.57	18.8	6.21	0.13	0.00	0.63	0.25
11	27.8	8.03	0.00	0.23	0.33	0.43	28.9	8.17	0.00	0.00	0.46	0.54
13	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
14	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

n/a indicates pools that were not measured for habitat variables due to logistic constraints

recede at a slower rate than flood one, which might allow greater settling time for small particles.

Fish habitat associations

There was no correlation between site correlations based on species abundance data and site correlations based on habitat variables on either date (5 June normalized $Z=-0.322$, $t=-1.4735$, $p=0.0703$; 8 July $Z=-0.24250$, $t=-1.2317$, $p=0.1090$). Thus, fish assemblages did not segregate based on measured habitat variables.

Discussion

Fish assemblages in flood prone lotic systems typically consist of species that are resistant and/or resilient to flooding (Poff and Allan 1995). Individual species traits vary within such assemblages, however, and relatively little is known about how such trait variation may affect assemblage response to flooding

at the local scale. In this study sequential large and erosive floods altered fish abundance and assemblage structure, but the magnitude and direction of change varied substantially among individual pools and fish species. Changes in assemblage structure within and among pools were driven largely by shifts in abundance and distribution of two dominant minnow species: bigeye shiners *N. boops* and central stone-rollers *C. anomalum*. These species exhibit shoaling behavior, and are often patchily distributed in large groups among pools (Power and Matthews 1983; Schaefer 1999). Because of this trait it is perhaps not surprising that these two species showed such dynamic shifts in abundance after floods, since roving groups seem more likely to cause large abundance shifts than scattered individuals of more territorial species.

In this study abundance shifts were sometimes drastic within individual pools following a flood, but there was no trend suggesting downstream displacement or upstream dispersal as the mechanism, though it is possible that some downstream displacement was

missed, since not all pools in the reach were sampled. Intense stream flooding can decimate the base of stream food webs by washing invertebrates and algae downstream (Power and Stewart 1987; Dodds et al. 2004), but fish responses to flooding may be more complex due to fish mobility (Franssen et al. 2006). In a long-term study of King's Creek, a prairie stream in Kansas, Franssen et al. (2006) found little evidence of downstream displacement of fishes, but instead noted that flooding allowed upstream movement of fishes to previously isolated or dry habitats. This study complements previous findings that floods in prairie streams may temporarily remove riffles barriers between pools, allowing movement among previously isolated habitats, but with little directional preference (Lonzarich et al. 2000; Franssen et al. 2006).

Fish assemblages can change irrespective of environmental disturbances, especially at the local habitat scale (Matthews et al. 1994). However, assemblage shifts in this study were likely directly related to flooding for several reasons. The first flood was short and more drastic than the second flood, and the magnitude of assemblage change in multivariate space appeared to correlate with flooding intensity (Fig. 2). Additionally, while assemblage shifts have been documented independent of disturbance events, they are rare compared to overall stability in these pools (Matthews et al. 1994). Finally, while Schaefer (1999) documented movement of bigeye shiners and central stonerollers among pools in Brier Creek at base flow, such movement was largely limited to a few individuals of each species. This is in contrast to the movement of large groups of these species (100's of individuals) among pools following flooding in the current study, suggesting that riffle barriers largely restrict movement of these species in Brier Creek, except during periods of high flow. Thus, the rapid and often drastic shifts seen in this study immediately following two separate flood events suggest that floods were the mechanism behind assemblage shifts in stream pools.

One mechanism by which flooding is predicted to alter fish assemblage structure is through disruption of fish-habitat associations (Matthews 1998). In this study I found no evidence that fish were associated with habitat variables before or after either flood. However, the deepest pools in the reach (>1 m) were not sampled. Such pools typically contain large

predatory bass and sunfish. Limiting samples to relatively shallow pools may have restricted the ability to detect habitat associations, especially if pool depth drives species distributions through a correlation with predator presence.

Flood effects in this study were assessed within days of a flood. Short-term flood effects in streams may persist when water levels drop and pools become isolated (Matthews and Marsh-Matthews 2007; Power et al. 2008). Winter flooding in the South Fork of the Eel River (California, USA) is typically followed by strong fish predation effects in summer, because flooding washes out large armored caddisflies, leaving vulnerable invertebrate assemblages (Power et al. 2008). In this study, bigeye shiners and central stonerollers showed dynamic population fluctuations among pools following floods. These species are important prey for large bass, and are typically negatively correlated with pools containing bass at base flow (Matthews et al. 1994), but large floods can redistribute these species among bass pools. If followed by increased predation when pools become isolated, flood redistribution patterns shown in this study may be an important factor in regulating population sizes of these species. Such residual effects of disturbance may be an important predictor of community structure in streams, but have received little attention (but see Power et al. 2008).

Species traits constrain the distribution and abundance of stream species along environmental disturbance gradients (Poff and Allan 1995; Townsend et al. 1997). Less studied is how trait variation within a local assemblage governs the response of assemblages to pulse disturbances such as flooding. This study demonstrates that the fish assemblage response to flooding is largely caused by the movement of two species with a shared behavioral trait (shoaling). I suggest that future studies consider the prevalence of shoaling species in a stream as a possible predictor of the response of local fish assemblages to environmental disturbances.

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Appendix 1

Table 4 Fish abundance in each pool based on snorkel counts on each sample date. Pools 5L/5U and 6/7 were considered a single pool on 21 May, but were sampled separately on 5 June and 8 July. Bass were split into juvenile and adult classes on 5 June and 8 July, but were not split on 21 May

Pool	21 May									TOT
	CANO	NBOO	FNOT	LMAC	LCYA	LHUM	LMEG	AMIC/JMIC		
2	0	300	0	20	0	0	30	0		350
5L	0	105	0	0	0	0	0	0		105
5U										
6	0	150	0	0	1	0	6	2		159
7	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a		n/a
9	0	50	0	0	0	0	57	0		107
11	0	20	0	0	0	0	0	1		21
13	0	100	0	0	0	0	18	0		118
14	0	70	0	0	0	0	50	1		121
Pool	5 Jun									TOT
	CANO	NBOO	FNOT	LMAC	LCYA	LHUM	LMEG	AMIC	JMIC	
2	10	18	0	17	0	0	4	0	0	49
5L	0	0	0	0	0	0	4	0	0	4
5U	0	52	0	2	0	0	5	0	0	59
6	0	10	0	0	0	1	0	1	0	12
7	0	0	0	0	0	0	4	0	0	4
9	217	32	0	4	0	9	41	0	0	303
11	30	43	1	0	0	0	22	0	0	96
13	3	0	1	0	0	1	22	3	0	30
14	0	0	0	0	0	0	9	2	0	11
Pool	8 Jul									TOT
	CANO	NBOO	FNOT	LMAC	LCYA	LHUM	LMEG	AMIC	JMIC	
2	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
5L	0	0	0	0	0	0	1	0	0	1
5U	0	120	0	4	0	0	22	0	0	146
6	0	0	0	4	0	0	2	1	2	9
7	30	0	0	2	0	0	0	0	0	32
9	0	0	0	0	0	0	69	0	3	72
11	0	50	0	0	0	0	5	0	3	58
13	0	0	0	0	0	0	19	0	0	19
14	36	22	0	0	0	0	6	0	0	64

JMIC juvenile bass (*Micropterus* spp., <100 mm), *AMIC* adult bass (>100 mm), *LMEG* *Lepomis megalotis*, *LMAC* *Lepomis macrochirus*, *LHUM* *Lepomis humilis*, *NBOO* *Notropis boops*, *FNOT* *Fundulus notatus*, *CANO* *Camptostoma anomalum*, *LCYA* *Lepomis cyanellus*

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