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Resilience of fishes and invertebrates to prolonged drought in two California streams

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Long-term data are needed to assess spatial and temporal variability of communities and their resilience to natural and anthropogenic disturbances, particularly in climatic regions marked by high interannual variability (e.g. mediterranean-climate). A long-term study at four sites on two streams in mediterranean-climate California (annual sampling over 20 yr) allowed us to quantify the influence of a 5-yr prolonged drought on stream invertebrate and fish communities. Invertebrate community composition did not show recovery following drought. The primary environmental factors influencing community composition, identified through principle components and multiple correspondence analyses were precipitation and flow permanence. Invertebrate taxon richness and abundance exhibited few responses (some site specific) and recovered quickly. Native fish abundance was lowest during the drought period and highest during the wet years that occurred at the end of the study period. Importantly, the prolonged drought facilitated the establishment and success of the invasive green sunfish (Centrarchidae: *Lepomis cyanellus*) that was then resilient to subsequent large flow events. There was high spatial synchrony in the temporal changes among all four sites, and three distinct periods were identified: early drought, late drought, and post-drought years. However, we still found differences among sites along the flow permanence gradient from temporary to perennial in the response to drought of both invertebrate and fish assemblages likely as a result of changes in substrate, vegetation, and other habitat characteristics. The observed lack of resilience and negative impacts to biodiversity due to prolonged drought associated with long-term habitat changes is important because hydroclimatic extremes are predicted to increase in frequency and magnitude with global climate change.

Droughts affect every continent on earth with diverse ecological impacts that depend on local factors such as climate and ecosystem type. In particular, multi-year or prolonged drought may have qualitatively and quantitatively greater effects on ecosystems than short droughts (Haddad et al. 2002, Magalhães et al. 2007). Freshwater ecosystems are particularly vulnerable to prolonged drought because suitable habitat and refugia may be severely reduced or eliminated for periods ranging from hours to years (Magoulick and Kobza 2003, Magalhães et al. 2007). Furthermore, human responses to drought-related water scarcity may exacerbate drought effects on biota. For example, water withdrawal from streams for agricultural use during dry years can reduce habitat connectivity, and may result in critical flow reductions (lack of oxygen, high temperatures, etc.). Such interactions are increasingly common in mediterranean-climate regions (Slaughter and Wiener 2007), where droughts are frequent and there is high interannual variability in rainfall (Gasith and Resh 1999).

Extreme climatic events are expected to increase as a result of global climatic change, including an increase in

drought frequency, duration, and/or intensity in many regions of the world (Beniston et al. 2007). For example, some temperate regions are predicted to become more “mediterranean” in climate, i.e. with more seasonal and interannual variation in precipitation (Beniston et al. 2007). In another example, the proportion of precipitation occurring as snowfall is predicted to decrease (as rainfall remains unchanged or decreases) in the western US; simultaneously, snowmelt is expected to occur earlier in the year with rising temperatures (Payne et al. 2004). These changes will also result in increased prevalence of seasonal and interannual drought that are characteristic of mediterranean-climate regions. Thus, understanding the effects of climatic variability on mediterranean-climate ecosystems may lead to a better understanding of potential future impacts of climate change in other climatic regions (Bonada et al. 2007).

The potential interactive effects of multiple natural and anthropogenic stressors (e.g. drought, climate change, and human water use) on ecosystems (Christensen et al. 2006) highlight the need for an increased understanding of each

stressor. In the case of drought, a long-term perspective is necessary because drought disturbances occur over a period of months to years (Holmes 2006). Despite the need for and insights gained from a long-term perspective (Holmes 2006, Hobbs et al. 2007), most ecological studies are short (Bêche 2005, Jackson and Füreder 2006), with a few notable exceptions (Daufresne et al. 2007, Durance and Ormerod 2007, Hobbs et al. 2007). For example, a survey of the recent stream ecology literature (1999–2005) revealed that 83% of studies were less than three years in duration (Bêche 2005), and only ca 7% exceeded 10 yr.

The objective of this study was to determine the long-term resilience of aquatic communities to prolonged drought in mediterranean-climate streams. In this study, we define resilience as the time to return to a “reference” state following a disturbance, often referred to as “engineering resilience” (van Nes and Scheffer 2007). This definition differs fundamentally from the broader concept of “ecological resilience” (which is defined by the amount of disturbance a system can absorb before being changed). Ecological resilience is difficult to measure in practice, and measures of engineering resilience may be reliable indicators of ecological resilience (van Nes and Scheffer 2007).

We analyzed 19–20 yr of annually collected fish and benthic invertebrate data from two northern California streams. The study period encompassed a prolonged drought period (5 yr) and several wet years. Specifically, we assessed: 1) the resilience (i.e. recovery from disturbance)

of invertebrate and fish communities to drought disturbance along a flow permanence gradient; 2) the spatial variability of temporal change of invertebrate communities and fishes across a restricted spatial scale ($< 30 \text{ km}^2$); and 3) the influence of prolonged drought on native and non-native fish species abundances.

Methods

Study sites

Invertebrates and fishes were sampled annually at four sites in Knoxville (site K1) and Hunting (sites H1, H2, H3) Creeks, in the Univ. of California Donald and Sylvia McLaughlin Natural Reserve (Napa and Lake Co.), California, USA (Fig. 1). These are small upland streams (watershed area: $2.1\text{--}29.3 \text{ km}^2$) and summer flow is either reduced but perennial (H2 and H3), intermittent (disconnected pools; H1), or dry (K1; Table 1). Watershed soils are mostly serpentine, and the riparian and upland vegetation is native shrub/chaparral and mixed native/naturalized grasslands.

Sampling methods

Mean flow ($\text{m}^3 \text{ s}^{-1}$) and conductivity ($\mu\text{S cm}^{-1}$) were measured at five points at the time of sampling and data were

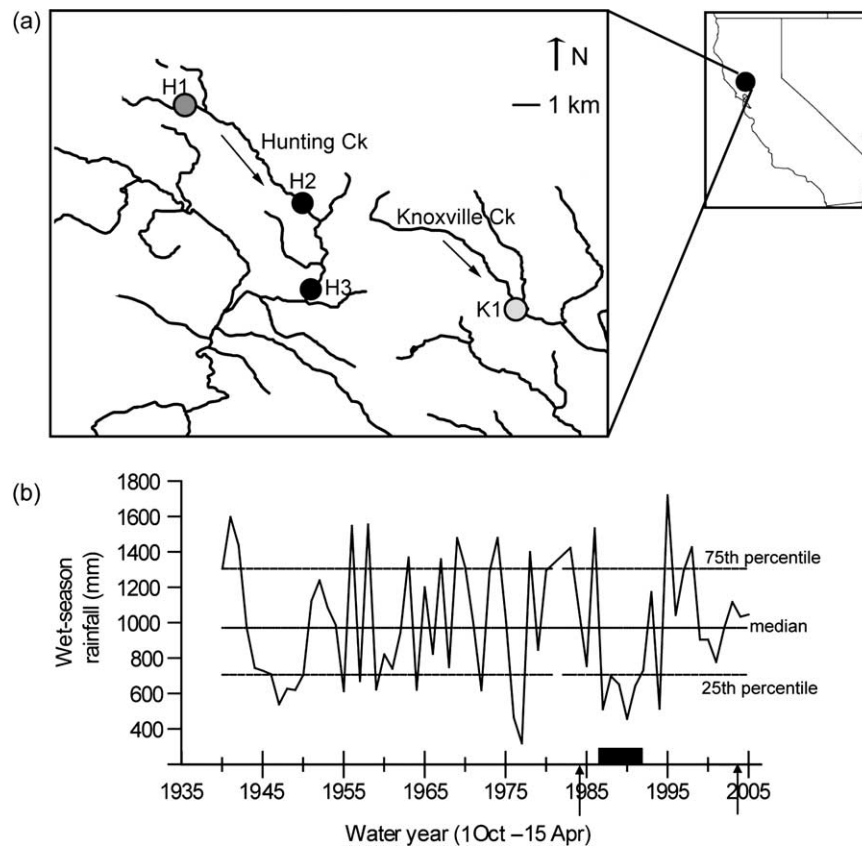


Figure 1. (a) Map of study sites (California, USA). Symbol colors indicate flow status of the site (light gray = ephemeral, dark gray = intermittent, black = perennial). (b) Wet-season rainfall at Angwin, California (1938–2004), indicating median, and 25th and 75th percentiles. The arrows indicate the sampling period (1984–2003), and the black box indicates the prolonged drought period (within 25th percentile).

Table 1. Characteristics of the study sites and summary of flow and habitat variables (mean \pm SD) pre- (1984–1986), during (1987–1991, 1994), and post-drought (1995–2003). Flow regime is based on dry-season flow: ephemeral (no water present), intermittent (disconnected pools), or perennial (flowing water). Instream vegetation cover is based on qualitative assessment of photographs (Supplementary material Fig. S1) and field notes. Substrate size was assessed in 1984 and 2003. CV = mean/standard deviation.

Flow regime	Site characteristics			Habitat by drought period		
	Catchment area (km ²)	% slope	CV flow (%)	Flow (m ³ s ⁻¹)	Conductivity (μ S cm ⁻¹)	Instream vegetation cover
Knoxville Creek K1 ephemeral	2.1	2.2	92.5	pre	2767 \pm 1933	very low
				during	3248 \pm 1115	moderate
				post	897 \pm 240	low
Hunting Creek H1 intermittent	4.4	1.5	149	pre	1428 \pm 838	very low
				during	1751 \pm 470	high
				post	617 \pm 129	very high
H2 perennial	22.1	1.6	110	pre	1220 \pm 1245	very low
				during	2765 \pm 2396	high
				post	712 \pm 166	low
H3 perennial	29.3	1.8	102	pre	2112 \pm 196	very low
				during	2227 \pm 547	high
				post	754 \pm 167	low
						Substrate size (mm) median (mean)
						64 (26)
						16 (38)
						16 (24)
						2 (10)
						64 (50)
						32 (78)
						64 (95)
						16 (48)

$\log_{10}(x+1)$ -transformed for analysis. Local precipitation was measured 1 km west of site K1 and was quantified as 1-month (15 March–15 April) and total wet-season (October–15 April) precipitation. 1-yr, 2-yr, and 3-yr lags in total wet-season precipitation were also used for analysis.

We noted changes in in-stream vegetation in annual reports and site photographs taken during site visits; however there are no quantitative measures. Substrate surveys (100 pebbles measured randomly along a 50–100 m reach) were conducted in 1984 and 2003.

We sampled annually at the end of the wet-season (ca 15 April \pm 5 d) from 1984 to 2003 for invertebrates (at site H1, sampling began in 1985) and from 1984 to 2002 for fish. Invertebrate samples (5 0.093 m², 0.5 mm mesh Surber) were taken in the same location each year and identification was to the lowest taxonomic unit, usually genus. Invertebrates occurring in only one year (35 taxa) were removed prior to analysis. Multiple-pass removal (3–4 successive electrofishing passes) was used to estimate fish abundance and individual fork length (mm) in four 30.5 m reaches at each site.

Identification of the drought period

We identified the duration and intensity of the drought period using data (1938–2004) from a nearby weather station (Angwin, CA, USA). Although precipitation was \sim 35% higher at Angwin than at the study site, annual trends in precipitation were similar (1984–2003, $R^2 = 0.91$, $p < 10^{-21}$). Years were classified as: wet, if precipitation was within the 75th percentile (> 1300 mm); dry, if within the 25th percentile (< 700 mm), and average for all other years. Severe drought and wet years were identified as years within the 10th (< 550 mm) or 90th percentile (> 1500 mm), respectively. Using these criteria, the five-year period from 1987 to 1991 and 1994 were identified as drought years ($n = 6$); 1987, 1990, and 1994 were classified as severe drought. Wet years ($n = 5$) included 1986, 1995, 1997–1998, and 2003; 1986 and 1995 were extremely wet years. Average years ($n = 9$) included 1984–85, 1992–93, 1996, and 1999–2002 (Fig. 1).

We assessed the magnitude of the drought and later floods using frequency analyses of U.S. Geological Survey flow data (1930–1932, 1934–2006) from a stream (Napa River at St. Helena, 4th order) ca 13 km west of the study area. The largest floods (maximum daily flow) during the study period were in 1997 (25-yr flood) and 1995 (10-yr flood). However, the mean monthly flows in January and March 1995 were 100-yr events (1% chance of occurrence in any given year).

The average return interval for the mean 3 month flow during the drought period (1987–1991, 1994) was 10 yr. However, the 5-yr consecutive drought had a recurrence interval of 75 yr, (1.3% chance of occurrence). We also identified 1982–1986 and 1995–1999 as the two wettest 5-yr periods on record (75 and 38 yr return intervals, respectively).

Data analysis

Invertebrate assemblages

We used linear mixed-effect models to assess the effects of site and precipitation (wet, dry, and average years), and

drought period (before, during, after) on invertebrate richness (number of taxa) and ln-transformed abundance (both variables taken as the mean of five samples taken in each year at each site). Two models were examined: 1) Site by DroughtPeriod and 2) Site by PrecipitationPeriod. Site, Drought, and Precipitation Period were treated as fixed factors and Year was included as a random variable. Planned contrasts among precipitation years and drought periods (all sites combined) were conducted (using the function “estimable” in the gmodels package for R, Warnes 2007). Post-hoc contrasts were conducted among precipitation years and drought periods for each site when their interaction term was significant.

To analyze changes in invertebrate composition, we performed three sets of multivariate analyses: 1) principal components analysis (PCA), 2) between-PCA, 3) multiple correspondence analysis (MCOA), and 4) indicator species analysis (ISA).

We used the Hellinger transformation on species abundances to improve the performance of the Euclidean distance used in PCA (Legendre and Gallagher 2001). The Euclidean distance of the transformed data (as calculated by PCA) was then equivalent to the Hellinger distance, which improves the representation of actual inter-community differences compared to other distance measures (e.g. chi-square distance) in ordination (Legendre and Legendre 1998).

We used a PCA of all sites together to examine the effects of a priori defined factors on community composition [sites, flow permanence, precipitation years, drought period (pre-, during, and post-drought)]. We used between PCA for all sites combined and for each site separately to assess the influence of one factor on community composition (i.e. a constrained PCA ordination). Site and flow permanence were examined for all sites combined, and precipitation years and drought period were examined for each site separately.

We used multiple correspondence analysis (MCOA) to assess the common temporal structure of the four study sites (1985–2003) and to examine temporal synchrony among sites. MCOA is a multi-table ordination approach that maximizes the covariance between individual ordinations of each site (using PCA) and a reference ordination (Bady et al. 2004, Daufresne et al. 2007). The reference structure obtained represents the common temporal structure shared by all sites. The goodness of fit of the reference structure was indicated by three statistics: 1) the squared cosines (\cos^2) of the angles between the first two axis scores of separate PCA for each site and the first two axes of the reference structure indicated the fit of the reference structure for each site; 2) the squared covariance (cov^2) between each separate ordination and the reference structure expressed the contribution of each site to the reference structure; 3) the RV coefficient (0 to 1) between each site matrix and the reference structure is a multivariate correlation coefficient indicating the strength of the relationship between the two tables (Robert and Escoufier 1976).

The importance of precipitation, temporal, and spatial influences on community composition were assessed by fitting vectors (or factors) to the PCA ordination and the MCOA reference structure using the function “envfit” in the “vegan” package for R. We used indicator species analysis (ISA; Dufrene and Legendre 1997) to identify the

taxa characteristic of the time periods before, during, and after drought. The indicator value of a taxon is the product of the relative frequency of occurrence and relative average abundance (multiplied by 100) in a priori defined groups (e.g. drought period). The ISA index is maximum (=100%) when all specimens of a taxon are found in a single group of samples and when the taxon occurs in all samples of that group. A taxon was considered an indicator of a particular drought period (before, during, after) when its indicator value was significantly higher than expected by chance (i.e. when compared to 1000 random samples of plots with the same number of species occurrences).

Fish assemblages

Fish count data for each site and year were standardized (number per 30.5 m reach) using the Leslie method (Leslie and Davis 1939), regressing catch-per-unit-effort (CPUE) against cumulative catch and calculating total estimated cumulative catch when $\text{CPUE} = 0$. When the data did not fit the Leslie method (i.e. $r > 0.7$) we used the Zippin method to make a maximum likelihood estimate of total abundance (Platts et al. 1983). Standardized fish densities were then square-root transformed (to meet assumptions of normality) prior to analysis. Roach, green sunfish, and Sacramento sucker were examined because they were the most abundant species and present in most ($\geq 85\%$) years. Multivariate analyses were not performed with the fish data because only three species were present at one site, and only one species was present at the other three sites. Changes in the abundance of roach, green sunfish, and sucker were analyzed using linear mixed effects models (as described above for invertebrates). Site was not included as a factor for green sunfish and sucker because they only occurred at site H3. Because fish populations often exhibit lags in their responses to environmental change, we also modeled (using ordinary least squares regression) the density of roach and green sunfish at each site as a function of previous year density and current and previous year flow.

All analyses were performed using the ade4 (Chessel et al. 2004), gmodels (Warnes 2007), labdsv (Roberts 2007), nlme (Pinheiro et al. 2008), and vegan (Oksanen et al. 2008) packages in R 2.7.1 (R Development Core Team 2008).

Results

Habitat changes associated with prolonged drought

During drought years, flow was reduced and conductivity increased; however, post-drought years were marked by increased flow and reduced conductivity. In contrast, median and mean substrate size decreased at all sites over the study period (Table 1). During the prolonged drought (1987–1991), aquatic macrophytes [primarily the sedges *Carex serratodens*, *Eleocharis macrostachya* and *Scirpus acutus* var. *occidentalis*, cattails (*Typha*), and the riparian willows (*Salix*)] increased in cover in Hunting Creek sites (Table 1, Supplementary material Fig. S1), reducing available aquatic habitat (area and volume) for invertebrates and fish. Floods during the post-drought wet period (particularly 1995 flooding) scoured away much of this vegetation at sites

H2 and H3 (Table 1). The ephemeral stream (K1) was too dry to support many macrophytes.

Impact of prolonged drought on invertebrate assemblages

Richness and abundance

Invertebrate taxon richness and total abundance of invertebrates differed significantly among sites in both models (Table 3, Supplementary material Fig. S2). In contrast, invertebrate richness and abundance did not differ significantly among precipitation years and drought period, although there was a significant site by precipitation year interaction for abundance (Table 3). Contrasts among precipitation years or drought periods for all sites combined were non-significant ($p > 0.05$). Site-specific contrasts were conducted for abundance (significant interaction terms); only dry versus average ($p = 0.003$) and wet versus average ($p = 0.035$) years and before versus during drought ($p = 0.047$) differed significantly at site K1.

Community composition

The PCA of all sites combined revealed gradients of flow permanence and 1-yr lag rainfall along PC 1 and total rainfall and year along PC 2 (Fig. 2, Table 2). In particular, differences in community composition between temporary (ephemeral and intermittent) and perennial sites were greater during drought years than during wet years, as

indicated by Euclidean distance (t-test, $t = 3.77$, $DF = 229$, $p = 0.0002$).

Between PCA revealed a strong influence of site (15.1% of the total variation, $p = 0.001$) on community composition, 7.8% ($p = 0.001$) of which was a result of flow permanence. Within each site, drought period explained more variation (K1 = 16.8%, $p = 0.002$; H1 = 22.5%, $p = 0.001$; H2 = 12.7%, $p = 0.036$; H3 = 15.9%, $p = 0.004$) relative to precipitation years (K1 = 15.0%, $p = 0.006$; H1 = 13.7%, $p = 0.068$; H2 = 12.7%, $p = 0.043$; H3 = 10.9%, $p = 0.337$).

The MCOA reference structure provided an adequate representation of the temporal structure of all four sites (high \cos^2 and RV, and similar cov^2 values; Fig. 3). The reference structure was highly correlated with 1-yr lag rainfall (axis 1, ns) and year of sampling and total rainfall (axis 2), similar to the unconstrained PCA of all sites (Fig. 2, 3, Table 2). No recovery from drought was evident based on MCOA. For example, three distinct temporal groups are evident from the MCOA reference structure: early (pre- and during-drought: 1985–1990), mid- (end of drought and immediately post-drought: 1991–1994), and late (post-drought: 1995–2003) sampling years (Fig. 3). We subsequently tested the influence of these temporal groupings on community structure at each site in between PCA analysis (K1 = 17.8%, $p = 0.001$; H1 = 22.7%, $p = 0.001$; H2 = 13.7%, $p = 0.012$; H3 = 16.7%, $p = 0.001$) and in ISA (see below).

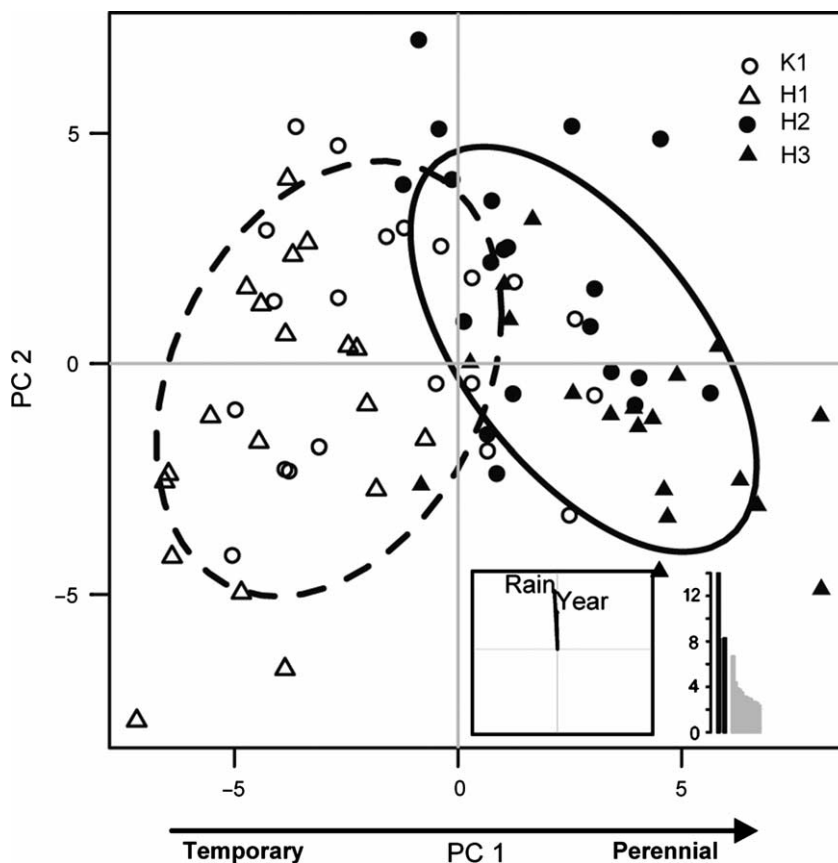


Figure 2. Unconstrained PCA of all sites showing differences attributed to flow regime (temporary – open symbols, perennial – closed symbols; ellipses enclose 70% of the data points) and site. The insets show the influence of total rainfall and year (Table 2) on community composition and the eigenvalues for the PCA ordination (the black bars are the two axes shown in the figure).

Table 2. Pearson correlation (r) of MCOA reference structure and separate PCA ordinations with year and rainfall. Significance is indicated as $p < 0.10$ (†), $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***) based on significance criterion adjusted (Bonferroni correction) for multiple tests.

	All sites PCA				MCOA reference			
	Axis 1		Axis 2		Axis 1		Axis 2	
	r	p	r	p	r	p	r	p
Year	-0.009	0.936	0.389	0.0004**	-0.154	0.528	0.880	10^{-7***}
Rainfall								
1 month	-0.045	0.695	0.460	10^{-5***}	0.411	0.081	0.210	0.387
Total	-0.039	0.734	0.603	10^{-9***}	0.275	0.254	0.610	0.006
1 yr lag	0.330	0.003†	-0.027	0.811	-0.563	0.012	0.306	0.203
2 yr lag	0.236	0.036	0.142	0.213	-0.365	0.126	0.085	0.729
3 yr lag	0.193	0.089	0.055	0.628	-0.004	0.986	-0.032	0.897

Pre-drought communities were characterized by the soldierfly *Euparyphus*, the water bug *Ambrysus*, and the caddisflies *Dicosmoecus* and *Marilia*, as determined by ISA among drought periods. Of the 24 significant indicator taxa

($p < 0.05$), 11 were indicators of the pre-drought period, 8 of the drought period, and 5 of the post-drought period. The taxa indicative of drought years included the caddisfly *Hydroptila*, the Dipteran *Palpomyia*, and the beetle *Deronectes*. The mayfly *Baetis*, the stonefly *Sweltsa* and the crane fly *Tipula* were significant indicators of the post-drought period. Using the MCOA defined periods, 30 taxa were significant indicators. The early period (17 indicator taxa) was characterized by *Euparyphus*, *Hydroptila*, and *Ochrotrichia*. The mid-period (8) was characterized by *Agabinus*, *Forcipomyia*, and *Tropisternus*. Finally, the late period (5) was characterized by *Ameletus*, *Baetis*, and *Sweltsa* (Supplementary material Fig. S3).

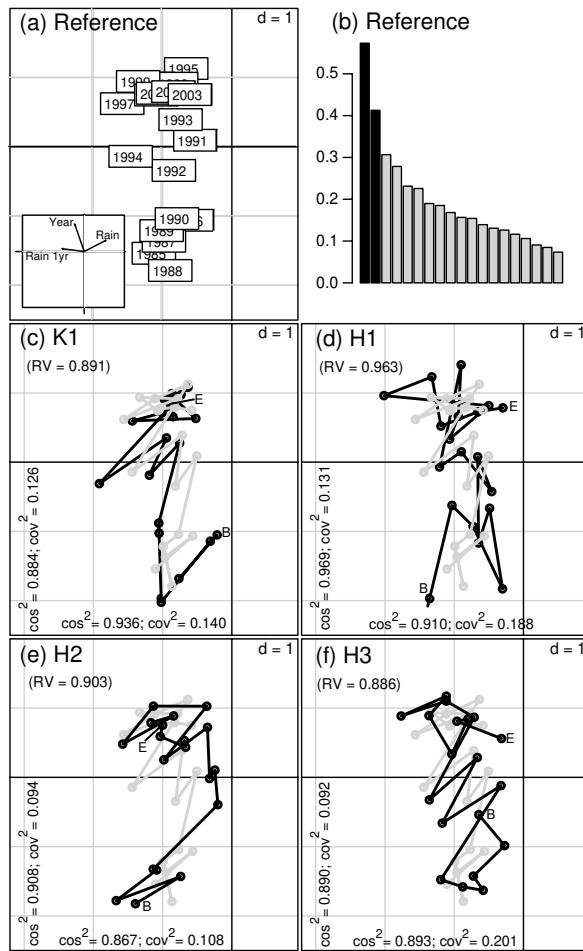


Figure 3. (a) MCOA reference temporal structure (1985–2003) of invertebrate community composition; the inset shows the influence of rainfall variables and year of sampling as indicated by vectors (Table 2); (b) barplot of the pseudo eigenvalues for the MCOA reference structure; (c–f) correspondence between temporal trajectory for each site (black line) and the reference trajectory (gray line). The beginning (B, 1985) and end (E, 2003) of the study period are indicated. Statistics for the goodness of fit of the reference structure of the MCOA at each site (\cos^2 , cov^2 , RV) are indicated and explained in the text.

Impact of prolonged drought on fish populations

Three native fish species were collected over 19 yr at the four study sites: California roach (Cyprinidae: *Lavinia symmetriscus*; collected 19 yr), Sacramento sucker (*Catostomus occidentalis*; 17 yr), and Sacramento squawfish (*Ptychocheilus grandis*; 5 yr); and one non-native species (green sunfish, Centrarchidae: *Lepomis cyanellus*; 18 yr). Roach were present at every site, but only site H3 consistently supported populations of green sunfish and sucker to examine assemblage patterns. Green sunfish was accidentally introduced to California in San Diego County in 1891 (mistaken as bluegill *Lepomis macrochirus*, Moyle 2002) and has since spread to every major drainage basin in the state. Green sunfish became established in Hunting Creek in 1987 from a downstream reservoir; prior to 1987, no population was established in the study reach and only transient individuals were found.

Abundance patterns

Roach abundance was lowest during the drought period (1988–1993) and highest during the last six wet years of the study (1997–2002), except at site H1. Roach abundance at site H1 decreased sharply over time ($R^2 = 0.50$, $p = 0.0004$; linear regression of abundance versus time), from 235 ± 168 (mean \pm SD) individuals in 1985 to 9 ± 5 individuals in 2002 (Fig. 4). Similarly, non-native green sunfish abundance increased over time at site H3 ($R^2 = 0.18$, $p = 0.04$) (Fig. 4). At the ephemeral site (K1), roach abundance declined to zero for 13 yr during and following drought (1986–1998), but recovered to or exceeded pre-drought abundance post-1998.

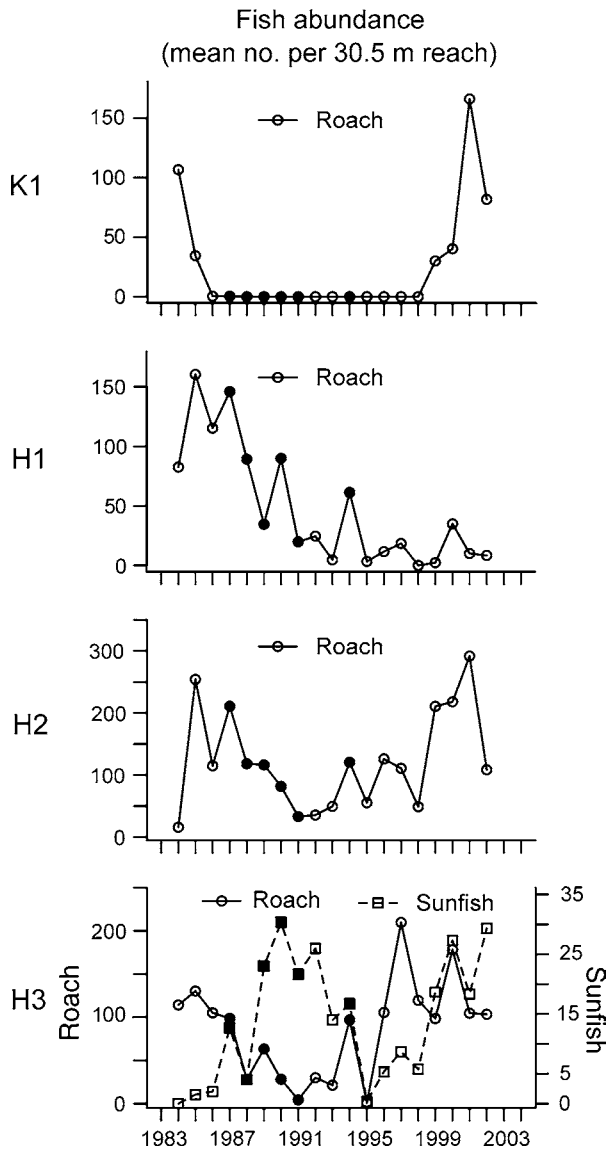


Figure 4. Mean yearly abundance per 30.5 m reach ($n=3-4$ transects yr^{-1}) of California roach (sites K1, H1, H2, and H3) and green sunfish (site H3). The drought years (1987–1991, 1994) are indicated by filled symbols and all other years are represented by open symbols.

Linear mixed-effects models of fish abundance demonstrated that changes in fish populations during the study period varied greatly among sites and species. For example, the greatest influence on roach abundance was site, and the effects of precipitation year and drought period were site-specific (Table 3, see above). With all sites combined, no contrasts among precipitation years were significant ($p > 0.05$). Abundance in the drought periods before versus after drought ($p = 0.012$) differed significantly when all sites were combined; abundance at site H1 before versus after ($p < 0.001$) and during versus after ($p < 0.001$) drought periods differed significantly.

Green sunfish abundance was not affected by precipitation period ($p = 0.092$, but differed significantly among drought periods (0.050). In particular, green sunfish abundance before versus after ($p = 0.049$) and before versus

Table 3. Summaries of linear mixed models for invertebrates (abundance and richness) and roach (abundance) (see text for more details). Asterisks indicate significance (no correction) of each model element at $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). The numerator degrees of freedom (num DF) is the same for all three models, whereas the denominator degrees of freedom (den DF) differs between the invertebrate and roach models because roach sampling was only conducted for 19 yr.

Model	num	den	Invertebrate taxon richness				Invertebrate abundance (ln)				Roach abundance (sqrt)			
			SS	MS	F	p	SS	MS	F	p	SS	MS	F	p
1) Precipitation (wet/average/dry years)														
Site	3	50	243	81.1	12.68	<0.0001***	7.8	2.6	7.95	0.0002***	649.4	216.5	24.7	<0.0001***
Precip	2	17	37.7	18.9	2.95	0.079	0.3	0.1	0.50	0.613	22.8	11.4	1.301	0.426
Site by Precip	6	50	14.3	2.4	2.39	0.893	6.1	1.0	3.09	0.012*	166.6	27.76	3.168	0.096
2) Drought period (before/during/after)														
Site	3	50	243	81	12.59	<0.0001***	7.8	2.6	7.4	0.000***	649.4	216.5	27.51	<0.0001***
Period	2	17	3	2	0.25	0.783	0.4	0.2	0.54	0.592	27.37	13.69	13.69	0.305
Site by Period	6	50	12	2.0	0.31	0.928	5.0	0.8	2.4	0.043*	209.5	34.91	34.91	0.040*

during ($p = 0.025$) drought differed significantly. These results confirm that green sunfish became established at the onset of drought and that their abundance increased during the drought. Furthermore, once established, population densities responded strongly to instream flow conditions (for example, abundance was greatly reduced during the 1995 floods and recovered in later “average” years; Fig. 4). In contrast, sucker abundance did not significantly change with precipitation years ($p = 0.325$) or drought period ($p = 0.711$), and no contrasts were significant ($p > 0.30$).

Roach and green sunfish density were significantly influenced by previous year density and either previous year flow (roach) or current year flow (green sunfish) at site H3. Roach density was not significantly related to previous or current year flow at sites H1, H2, and K3, but previous year density was a significant predictor for current year density at site H1 (Table 4).

Discussion

Invertebrate responses to prolonged drought

Our study confirms the conclusions of a recent review (Dewson et al. 2007) that droughts have equivocal effects on the abundance and richness of invertebrate communities. For example, drought may reduce (via reduced habitat suitability, particularly in already water-stressed temporary habitats), or increase (e.g. via a concentration effect, as in the perennial sites of our study) invertebrate abundance. Taxon richness responded primarily to high precipitation (and thus, flows), and this effect was site-specific.

Temporal synchrony in the effects of prolonged drought on invertebrate community composition was observed across the study sites despite differences in the magnitude of these responses among sites differing in flow permanence. The observed synchronous changes in community composition over time as a result of the same environmental stressor (drought) are relative (i.e. communities differed in initial composition among sites, and although directional change was observed at each site, patterns of individual taxa may not be synchronous). Because the prolonged drought resulted in directional change in community composition (Bêche and Resh 2007), there was no evidence of invertebrate “recovery” from drought (i.e. no return to a pre-drought community composition). There is clearly little change in community composition after 1995, indicating post-drought stability resulting perhaps from the uninterrupted post-drought wet period (Bêche and Resh 2007).

We emphasize that both severity and duration are important in determining the outcome of drought on aquatic communities. Compared to acute droughts (<1 yr duration), prolonged droughts are more likely to result in persistent habitat changes, to reduce the sources of nearby potential colonists characteristic of higher flows, and to cause some local populations to disappear because of a lack of suitable habitat (Lake 2003). Evidence of the latter occurring during the study period includes the complete absence at the end of the study period of many taxa present at the beginning (e.g. *Dicosmoecus*, *Ambrysus*).

Table 4. Summaries of multiple regression models of fish densities at each site, with parameter estimates (Est \pm SE), and partial p -values. The overall adjusted R^2 (R^2_{adj}) and significance is presented. Density and flow (in $m^3 s^{-1}$ at the time of fish sampling) parameters are presented as current year (y_i) or previous year (y_{i-1}).

	K1		H1		H2		H3 (roach)		H3 (green sunfish)	
	Est (\pm SE)	p	Est (\pm SE)	p	Est (\pm SE)	p	Est (\pm SE)	p	Est (\pm SE)	p
Intercept	-4.6 \pm 15.7	0.774	13.4 \pm 18.7	0.487	88 \pm 42	0.054	16.1 \pm 17.7	0.379	6.6 \pm 4.6	0.168
Density (y_{i-1})	0.51 \pm 0.20	0.027	0.67 \pm 0.21	0.006	0.16 \pm 0.22	0.488	0.64 \pm 0.16	0.001	0.63 \pm 0.21	0.0082
Flow (y_i)	-110 \pm 1798	0.952	-345 \pm 243	0.178	-216 \pm 224	0.352	-262 \pm 94	0.014	-35.4 \pm 19.9	0.0967
Flow (y_{i-1})	2247 \pm 1777	0.227	303 \pm 256	0.256	464 \pm 219	0.052	403 \pm 88	0.0004	32.4 \pm 21.0	0.1443
	$R^2_{adj} = 0.245$, $p = 0.076$		$R^2_{adj} = 0.407$, $p = 0.016$		$R^2_{adj} = 0.115$, $p = 0.205$		$R^2_{adj} = 0.631$, $p = 0.0006$		$R^2_{adj} = 0.371$, $p = 0.023$	

Invertebrate communities tend to exhibit rapid recovery (usually within one year) following acute drought in regions ranging from mediterranean-climate Australia (Boulton 2003, Lake 2003) to chalk streams in England (Wright et al. 2004), which may be a result of the short-term nature of acute droughts. In contrast, Mouthon and Daufresne (2006) found no recovery of invertebrate communities one year following an acute drought in France. Their study ended one year post drought, making it impossible to determine actual recovery time (if any). Likewise, there were no pre-drought data for two studies examining prolonged drought effects on English chalk streams that reported recovery from prolonged groundwater drought after two years (Wood and Petts 1999, Wood and Armitage 2004).

Fish responses to prolonged drought

Responses to prolonged drought were species and site-specific (Matthews and Marsh-Matthews 2003, Magalhães et al. 2007), with effects being positive (green sunfish), neutral (sucker), or negative (roach). During drought, roach survival and reproduction are likely to be affected by increased competition, predation, and dry-season habitat loss (Gasith and Resh 1999, Magalhães et al. 2007). Roach recovered relatively rapidly (1–2 yr) in the permanent sites, but recovery was either delayed or non-existent in the ephemeral and intermittent sites, respectively. Similarly, Magalhães et al. (2007) found that fish community recovery from drought in Mediterranean-climate Spain differed according to an upstream-downstream gradient of flow permanence and habitat variability. In our study, delayed drought recovery of roach may be a result of the cumulative effect of drought over time (Magalhães et al. 2007), where already low summer flows were increasingly diminished as drought continued because of reduced recharge. Unless populations are extirpated (ephemeral site), or habitat is irrevocably altered (intermittent site), fishes are expected to recover quickly from drought once adequate flows resume (Magoulick and Kobza 2003, Davey and Kelly 2007); thus, severe drought (prolonged or acute) generally does not have long-lasting effects on fish communities (Matthews and Marsh-Matthews 2003).

The appearance and rapid success of the non-native green sunfish coincided with prolonged drought. We cannot causally link the drought with the establishment of green sunfish in Hunting Creek, however, only transient individuals were present in previous years (average to wet rainfall; based on collected data and pre-study site surveys), providing some evidence that the drought may have facilitated the establishment of this non-native species by creating more favorable habitat conditions. There is a strong relationship between disturbance and invasion success for various ecosystems (Eby et al. 2003, Altman and Whitlatch 2007, Hobbs et al. 2007), suggesting that the pattern of invasion following drought may not be limited to our study or ecosystem (Eby et al. 2003, Hobbs et al. 2007). Establishment of non-native species following naturally or anthropogenically altered flow regimes has been documented for both fish (Marchetti and Moyle 2001, Eby

et al. 2003) and invertebrate (Mouthon and Daufresne 2006) communities. Natural flow regimes tend to favor native species (Lytle and Poff 2004), but only if the invader differs ecologically from the native species (e.g. the “unlike [or unique] invader” hypothesis of invasion, Alpert 2006). However, when a non-native species has a similar ecology as a native species, success depends largely on superior competitive ability and/or predation on native species (Ayala et al. 2007). Green sunfish have a wide ecological and physiological tolerance similar to roach (Moyle 2002), and is both a competitor and predator of roach.

What can we learn from natural droughts?

Having a long-term perspective on the effects of droughts on ecosystems allows us to put these impacts into a larger context of environmental variability, climatic cycles and global climate change (Hobbs et al. 2007). Droughts are an important part of the dynamic flow regime in natural streams, influencing the evolution and adaptation of aquatic organisms (Lytle and Poff 2004), yet they are relatively understudied (Lake 2003). Evidence is growing that climatic change and hydroclimatic extremes (such as prolonged drought) can result in gradual changes or dramatic shifts in freshwater communities and assembly processes (Bady et al. 2004, Bêche and Resh 2007, Chase 2007, Daufresne et al. 2007, Durance and Ormerod 2007). When combined with increasing human demand for water exacerbated by climate change (Slaughter and Wiener 2007, Barnett et al. 2008), droughts may have increasingly dramatic effects on freshwater ecosystems and other closely coupled ecosystems (e.g. estuaries, riparian zones, etc.). In particular, flow reductions may reduce ecological resilience (Davey and Kelly 2007) to further hydroclimatic extremes or other anthropogenic stressors (Daufresne et al. 2007). By understanding the effects of multi-year droughts on aquatic systems we can begin to anticipate, and hopefully mitigate potential impacts of future climate change and related stressors (e.g. water abstraction) on stream biota (Payne et al. 2004).

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