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MEDITERRANEAN CLIMATE STREAMS **Review Paper**

Long-term population and community patterns of benthic macroinvertebrates and fishes in Northern California Mediterranean-climate streams

Vincent H. Resh · Leah A. Bêche · Justin E. Lawrence · Raphael D. Mazor · Eric P. McElravy · Alison P. O'Dowd · Deborah Rudnick · Stephanie M. Carlson

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Abstract Long-term studies can document temporal patterns in freshwater ecosystems, and this is particularly important in mediterranean-climate (med-climate) regions because of strong interannual variation in precipitation amounts and consequently stream flow. We review long-term studies of populations and communities of benthic macroinvertebrate and fishes from sites throughout the med-climate region of California and develop generalities that may apply broadly to med-climate streams worldwide. Severe drought may result in community shifts, and alter age-structure in both macroinvertebrates and fishes. Within-year seasonal patterns in macroinvertebrate communities can be influenced by annual variability in flow regimes. Macroinvertebrate biological-monitoring metrics with consistently low intra-annual variability may be especially applicable in med-climate streams, as is the use of different temporal windows to describe reference periods to reduce influence of interannual variability on impact detection. Long-term data can be used to develop macroinvertebrate-based metrics that can either show or be independent of climate-change effects. Most macroinvertebrate species are temporally rare in their annual occurrence. Multiple components of natural flow regimes can favor native over invasive fishes. Long-term, quantitative information from med-climate streams is generally lacking, which is a hindrance to both

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V. H. Resh (✉) · L. A. Bêche · J. E. Lawrence ·
R. D. Mazor · E. P. McElravy · A. P. O'Dowd ·
D. Rudnick · S. M. Carlson
Department of Environmental Science, Policy &
Management, University of California, Berkeley,
CA 94720-3114, USA
e-mail: resh@berkeley.edu

Present Address:
L. A. Bêche
Villeurbanne, France

Present Address:
R. D. Mazor
Southern California Coastal Water Research Project, 3535
Harbor Blvd Suite #110, Costa Mesa, CA 92626, USA

Present Address:
A. P. O'Dowd
Department of Environmental Science & Management,
Humboldt State University, Arcata, CA 95521-8299, USA

Present Address:
D. Rudnick
Integral Consulting Inc, 411 1st Avenue S., Suite 550,
Seattle, WA 98104, USA

management practices and development of appropriate ecological constructs.

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Introduction

Ecological studies of benthic macroinvertebrates and fishes in streams have been conducted informally as part of human survival for millennia. The inclusion of long-term observations on abundance and occurrence of aquatic biota clearly were critical elements that determined the establishment and persistence of civilizations (Resh & Rosenberg, 2010). With the onset of formalized ecological studies, however, most research described results from single observations or from patterns evident from observations made over short-time periods. Even today, only a small number of ecological studies are conducted to collect more than a few years of data (Resh & Rosenberg, 1989; Rosenberg & Resh, 1993; Elliott, 1993, 1994; Jackson & Füreder, 2006). However, since essentially all ecological patterns are temporally variable, the need for long-term data in ecological studies is obvious and has been documented repeatedly (e.g., Connell & Sousa, 1983; Elliott, 1990; Brook & Bradshaw, 2006; Jackson & Füreder, 2006; Burt et al., 2008; Dodds et al., 2012). Moreover, the potential for interactive effects among natural and anthropogenic stresses (e.g., drought, climate change, and water withdrawals) highlight the importance of long-term perspectives in understanding and assessing ecological conditions of stream and rivers worldwide.

Temporal changes in populations and communities of freshwater biota may occur within years (i.e., seasonal variability) or among years (i.e., annual variability). Both structural and functional changes typically are driven by short-term environmental factors that vary over the course of a year, such as rainfall (and consequent changes in stream flow), temperature, and food availability (e.g., leaf litter). The influence of seasonal variability on the structure of stream communities has been well studied in all types of stream ecosystems (e.g., Linke et al., 1999; Bonada, 2003; Matthews & Marsh-Matthews, 2003; Bêche et al., 2006).

In contrast to seasonal variability, annual variability results from inter-year changes in climatic features such as precipitation and temperature. Depending on the length and timing of the study, annual variability may also include extreme events, such as prolonged droughts or major floods, or more frequent natural phenomena that operate on multi-year cycles, such as El Niño- or La Niña-related changes in the magnitude, timing, and variability of precipitation. These complex climatic patterns may be an especially important source of variability in stream populations and communities. For example, El Niño conditions often intensify wet and dry cycles, and have been linked to changes in abundance, composition, and persistence of stream communities, such as benthic macroinvertebrates (e.g., Bradley & Omerod, 2001; Briers et al., 2004; Durance & Ormerod, 2007, 2009) and fishes (Mol et al., 2000; Puckridge et al., 2000; Lake, 2003; Bond et al., 2008). Moreover, annual variation produces temporal fluctuations in stream flow and in habitat quality and quantity both within a year and between years (Bêche et al., 2006). Consequently, annual variations in flow and habitat are well known to have strong influences on macroinvertebrates (e.g., McElravy et al., 1989; Bradley & Ormerod, 2001; Milner et al., 2006) and fishes (Oberdorff et al., 2001; Eby et al., 2003). Likewise, long-term temperature changes have also had a strong influence on community structure (Daufresne et al., 2004, 2007, 2009; Durance & Ormerod, 2007, 2009).

Seasonal and annual variability in community structure is often high in streams (Poff & Allan, 1995; Townsend et al., 1997; Daufresne et al., 2004) and is the greatest in regions with high environmental variability, such as mediterranean-climate (med-climate) regions (Boulton et al., 1992). In northern California, for example, flow regimes vary greatly between spring and summer, creating distinct community profiles (Bêche et al., 2006, 2009; Bonada et al., 2006; Bêche & Resh, 2007a, b). Furthermore, med-climate regions are characterized by extended periods of elevated flows during and immediately following the wet season, gradually shifting to long periods of reduced flows during the dry season (Gasith & Resh, 1999). During some years, extreme reductions in flows, i.e., droughts, can occur in all med-climate regions (Lake, 2008). Suitable habitat and refuges in freshwater systems may be severely reduced or limited as a result of prolonged drought (Lake, 2000, 2003). Moreover, human activities (e.g., groundwater withdrawal and water diversions) can further reduce habitat connectivity and increase the likelihood of elevated temperatures, low oxygen, and other factors that stress stream biota during drought (Gasith & Resh, 1999; Lawrence et al., 2011). Multi-year droughts may have qualitatively and quantitatively greater effects on ecosystems than short-term droughts (Haddad et al., 2002; Magalhães et al., 2007).

The purpose of this review article is to describe principles that emerged from a series of long-term ecological studies conducted on benthic macroinvertebrates and fishes in med-climate streams in California over the past three decades. We focused on this med-region because it is where most long-term studies have been performed, but we believe that the findings from this region can be applied to other med-climate and highly seasonal environments. Lessons learned from these research projects are used as title subheadings.

Description of available information

The nine major study sites and scores of publications reviewed in this article are geographically distributed at sites throughout the med-climate region of California (Fig. 1; Table 1; see Ball et al., 2012, for a description of med-climate regions of California). Most sites are located in the coastal region (except Blodgett Forest, BF). All sites have highly seasonal, and annually variable, rainfall (Fig. 2). Sites include: streams originating from spring seepages (Hopland Springs [HOP] and Big Sulfur Creek [BSC]); streams restored from underground channels (Baxter Creek, BC); streams with different seasonal flow regimes ranging from non-perennial to perennial (Knoxville Creek [KC], Hunting Creek [HC], Putah Creek [PC], and Russian River tributaries [RR]); and large-scale stream networks with estuarine influence (San Francisco Bay Area streams, SFBA). The multiple BF streams examined are located in the central Sierra Nevada mountain range and have a snowmelt-dominated hydrology.

Because sampling inconsistency (Needham & Usinger, 1956) and taxonomic errors (Lenat & Resh, 2001) are well-known sources of error and bias in benthic macroinvertebrate research, we have tried to minimize these sources of variability in several of the long-term studies described in Table 1. For example, the 20-years studies conducted at some of the areas examined (HOP, KC, HC, PC) are the most consistent long-term datasets for benthic macroinvertebrates available worldwide in that all collections were made by the same person, as were all identifications. In some other studies we included, collections and identifications were either made by two different people (BSC, BF), but for large-scale studies (SFBA) and long-term fish studies (PC, RR) multiple collectors were involved.

In the studies presented below, we have used all information available to us from med-climate regions worldwide for comparisons. However, the lack of such long-term data from other med-climates, especially for benthic macroinvertebrates, prevents broad comparisons between the California med-climate region and other med-climate regions. Long-term data for benthic macroinvertebrates and fishes from non-mediterranean areas do exist (e.g., Elliott, 1993; Rose et al., 2008; Chessman, 2009; Wagner et al., 2009; Chessman et al., 2010) and we are pleased to learn that long-term studies for other mediterranean regions (med-regions) have been initiated.

Population-level studies

Recovery of population age-structure following severe drought may require a decade

Small streams may experience periodic or regular loss of habitat as a result of the high interannual variability of precipitation that occurs in med-climates. Drying of stream beds can vary spatially within a stream and among nearby streams, and can vary temporally, even for similar sized streams in the same area. For example, among the small streams examined during long-term studies of HC and KC, the first-order KC went completely dry every year, whereas a nearby first-order HC site went dry once in 20 years. Extreme events, however, can affect stream habitats that normally remain permanent. In a spring seepage at HOP, a severe drought that occurred in 1976–77 resulted in cessation of stream flow and complete loss of the aquatic habitat for over three months (Resh, 1982). Fortuitously, collections had been made prior to the loss of habitat so that the recovery of the population could be followed over time.

Surveys before and after the loss of habitat from this drought indicated that the age-structure of the

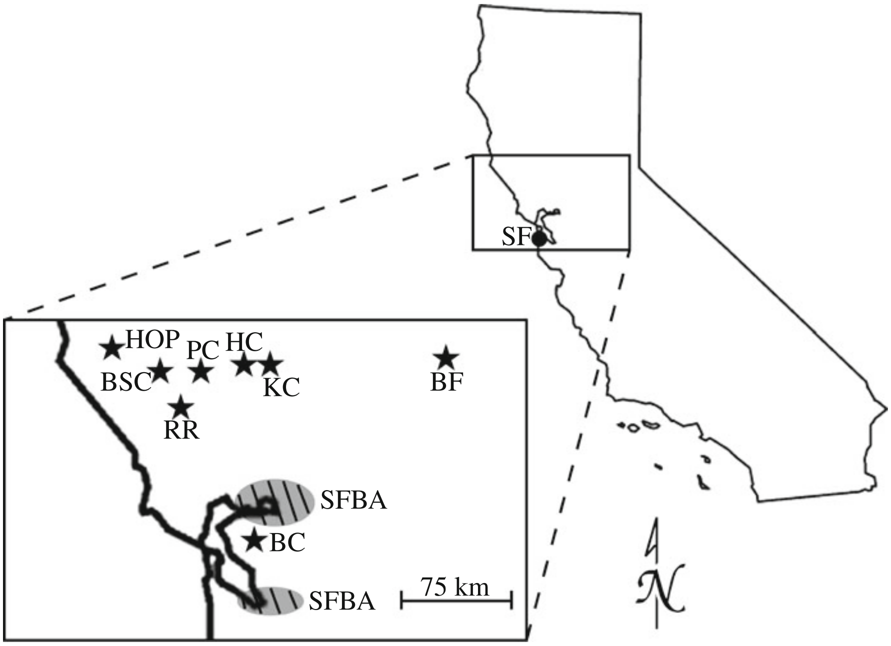

Fig. 1 Map of study sites in the med-climate region of California (see Ball et al. this issue for description of the med-climate region in this state). Stars indicate study sites: Hopland Springs (*HOP*), Hunting Creek (*HC*), Knoxville Creek (*KC*), Big Sulfur Creek (*BSC*), Blodgett Forest (*BF*), Baxter Creek (*BC*), San Francisco Bay Area streams (*SFBA*), Putah Creek (*PC*), and Russian River tributaries (*RR*). *Circle* indicates the location of the city of San Francisco (SF)

Table 1 Description of study sites in the med-climate region of California

Name of stream	Number of sites studied	Duration of study	Stream orders	Detailed site description
Hopland Springs (HOP)	2	10 years	1	Resh (1982, 1992)
Hunting Creek (HC)	3	19–20 years (1984–2003)	1–2	Bêche et al. (2006, 2009)
Knoxville Creek (KC)	1	20 years (1984–2003)	1	Bêche et al. (2006, 2009)
Big Sulfur Creek (BSC)	2	7 years (1977–1983)	3	Lamberti & Resh (1983); Bêche et al. (2006); McElravy et al. (1989)
Blodgett Forest (BF)	5	8 years (1995–2004)	1–2	Bêche & Resh (2007a, b)
Baxter Creek (BC)	1	Periodically over 10 year period	1	Purcell et al. (2002); Chin et al. (2009)
San Francisco Bay Area streams (SFBA)	>100	Periodically over 15 year period	1–3	Rudnick et al. (2000, 2003)
Putah Creek (PC)	8 sites; 6 sites	5 year period (1994–1998); 17 year period (1991–2008, except 1992)	4–5	Marchetti & Moyle (2001); Kiernan et al. (2012)
Russian River tributaries (RR)	1–3 reaches per tributary, including 50–55 pools per year	9 year period (1994–2002)	3–4	Grantham et al. (2012)

Stream location is found in Fig. 1

population of the caddisfly *Gumaga nigricula* changed dramatically from its original composition, and that the recovery to an age distribution similar to the original took over a decade (Resh, 1982, 1992). Monthly collections (1975–1976) from this stream indicated that the age-structure of the population prior

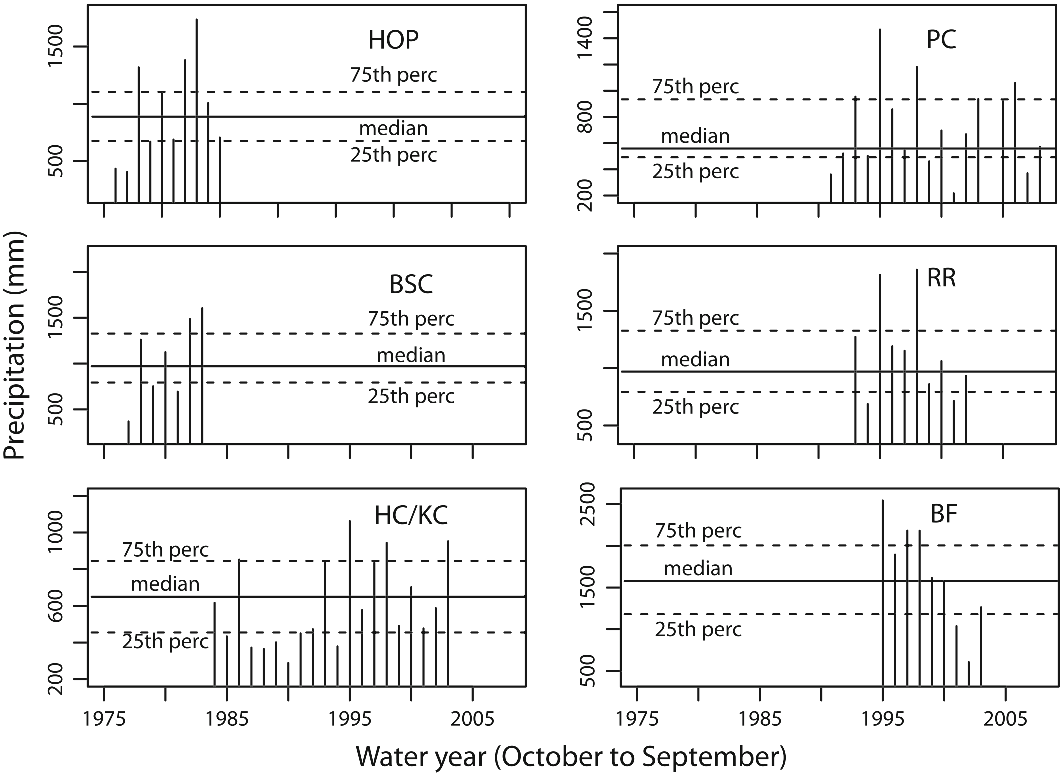

Fig. 2 Annual precipitation for each water year (October of the previous calendar year to September of the following year) during the time period that studies were conducted at the different sites listed in Table 1. The median, 25th, and 75th percentile values are based on long-term time series for the same sites. For each site, the weather station and the years of available precipitation data (used to calculate long-term precipitation statistics) are indicated. HOP: Hopland Field Station (1952-2010 water years); BSC: Healdsburg, CA weather station (1932-2010); HC/KC: McLaughlin Natural Reserve (1984-2003) plus Angwin, CA weather station (1938-2003); PC: Cache Creek USGS Weather Station (1988-2008); RR: Healdsburg, CA weather station (1932-2010); BF: Blodgett Forest Research Station (1962-2003)

to the drought that started in 1976 was dominated by early instars with pupae present year-round, reflecting a multi-cohort population. Surveys following resumption of flow indicated that no *G. nigricula* larvae survived this drought. In 1979, 2 years after habitat recovery, surveys indicated that although this species had recolonized, the age-structure had changed. A single-cohort population is now present, and a clear succession in the numerical dominance of age classes proceeding from early to late instars was evident over time (Fig. 3).

The likely mechanism of this change was temporally restricted, aerial recolonization from a population of *G. nigricula* from a spring 0.5 km away that was less affected by the 1976 drought and continued to flow. The post-recolonization density was quite low and presumably reflected temporally restricted oviposition by only a few individuals. Thus, the shift from a

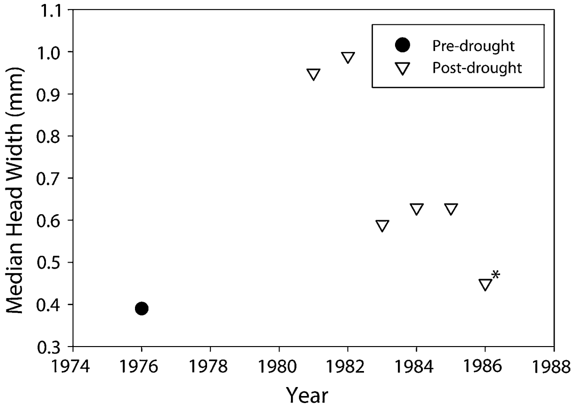

Fig. 3 Temporal changes in head capsule width for *Gumaga nigricula* before (1976) and after (1981-1986) the loss of its habitat as a result of extreme drought (data from Resh, 1982, 1992). $^{*}\chi^2$ not significantly different from 1976 pre-drought value; *t* test, *p* value of <0.001

multi-cohort to a single-cohort population occurred within 1 year, but the shift back to a multi-cohort population took much longer. Only in 1986, 10 years after the loss of habitat, did the population return to a multi-cohort age-structure similar to that present prior to the drought (Fig. 3).

This long recovery period could have been the result of drought-induced population density decrease or the lack of food availability. For example, prior to habitat loss, densities were >10,000 individuals/m^2 (Resh, 1982); following habitat loss, densities were on the order of 10 individuals/m^2, only gradually increasing to >1,000/m^2. Consequently, gradual increases in population density could allow the age-structure to spread out. Food limitation may also have resulted in all individuals growing at similar rates, as opposed to differential growth rates present in cohort splitting that would have resulted in the faster development of a multi-cohort population. *G. nigricula* also has the unusual ability among macroinvertebrates of going through a large number of molts without an associated increase in body size (Resh et al., 1997).

Recovery from disturbance is typically assumed to occur rapidly in populations and communities that regularly experience disturbance (Resh et al., 1988; Resh, 1992). However, the size distribution (or size spectrum) within the population, which is a reflection of age-structure, is rarely considered in assessing opportunities for population recovery. This study of the loss and recovery of a macroinvetebrate population in a med-climate region stream highlights the role of interannual variability in governing population dynamics and emphasizes that populations, even though they regularly experience stresses, may still be vulnerable to extreme events and the effects can be long lasting.

Age-structure shifts in fishes can occur from increased biotic interactions following drought

Changes in population structure of fishes as a result of drought, including their age-structure, have been poorly documented (Lake, 2003). However, as with benthic macroinvertebrates, some illustrative examples exist for fishes such as an experimental reduction in flow (in a non-med-climate stream) that led to a shift toward small individuals (Walters & Post, 2008). In med-climate streams of California, flow reductions are also accompanied by increases in water temperature and thus we might also expect a shift toward smaller fishes in these systems because large individuals have relatively higher metabolic demands than smaller conspecifics. However, stronger biotic interactions (especially size-selective predation) might lead to deviations from this expectation. In HC, for example, California roach (*Hesperoleucus symmetricus*) and green sunfish (*Lepomis cyannelus*) are the most abundant species that were present during most (89–100%, respectively) years (Bêche et al., 2009), are both affected by drought, and have ecological interactions that occur between them. Studies indicated that roach age-structure was affected by long-term patterns in flow that were driven primarily by flood and drought periods. For example, mean size of roach in a first-order HC site was low in pre-drought years (1984–1988), increased during the drought period (1989–1994), and then decreased again post-drought (1995–2002) (Fig. 4). A shift from a population dominated by smaller individuals to larger individuals coincided with the onset of the prolonged drought period. This shift indicated either low recruitment or low survival of young fishes as a result of drought.

Recovery time for fishes may be long, just as described above for benthic macroinvertebrates. Native roach populations took from 2 to 5 years after the last year of drought to recover in abundance at two HC sites, and no recovery in the population was observed at the first-order HC site as a result of dramatic habitat changes that occurred (Fig. 5, and see comments on regime shift below). This delayed, drought-recovery may be a result of the cumulative effect of drought over time on population structure and fecundity, similar to what was found in med-climate streams in Portugal (Magalhães et al., 2007) following an extended drought.

Prolonged drought likely affected recruitment and/or survival of both roach (negatively) and green sunfish (positively). In dry years and years following, the size distribution of roach was dominated by larger individuals, indicating reduced reproductive output and/or young-of-the year survival from stream drying, competition, and/or predation. In contrast, the age-structure of green sunfish seemed to be relatively unaffected by drought years despite strong correlations between these events and green sunfish abundance. However, an increase in young-of-the-year was noted following the extended drought (i.e., the opposite response of roach) (Fig. 4).

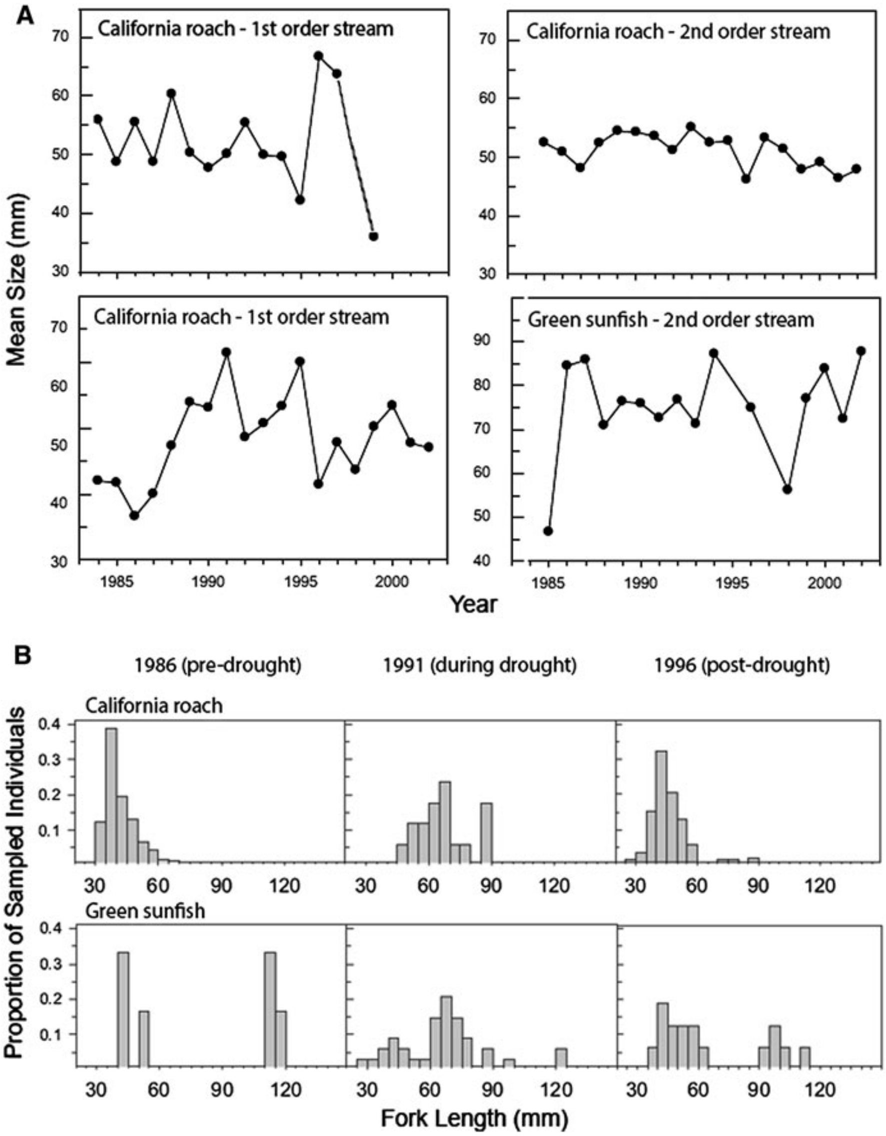

Fig. 4 **A** Annual changes in mean size for California roach at three sites, and green sunfish at one site. **B** Size distribution of both species in 3 years found at one second-order stream, demonstrating pre-drought (1986), drought (1991), and post-drought (1996) population patterns (data from Bêche et al., 2009)

Recruitment and juvenile survival may be the major factors influencing abundance patterns following drought. In the above example, both roach and green sunfish exhibited strong relationships to the previous-year rainfall (1-, 2-, and 3-year lags; Bêche et al., 2009), reflecting their relatively long life cycle (Moyle, 2002). During low flow years, roach and green sunfish populations are concentrated in the remaining pools that are partially or entirely isolated hydrologically. Here, both intra- and inter-specific (where applicable) competition could reduce population abundances (e.g., Labbe & Fausch, 2000). In addition, reduced summer survival as a result of habitat loss (e.g., Magalhães et al., 2007) and increased predation by green sunfish (when present) likely contributed to decreases in roach abundance in dry years. However, roach abundance was relatively high in 1994 (a severe drought year) as a result of high recruitment during the previous wet year.

Habitat availability that reflects interannual variation in flow regimes may influence interactions among fish species and consequent age-structure. During high flow years, roach reproductive output likely increased (e.g., Cattanéo et al., 2002; Moyle, 2002) as habitat availability increased and consequently biotic pressures from competition and predation decreased

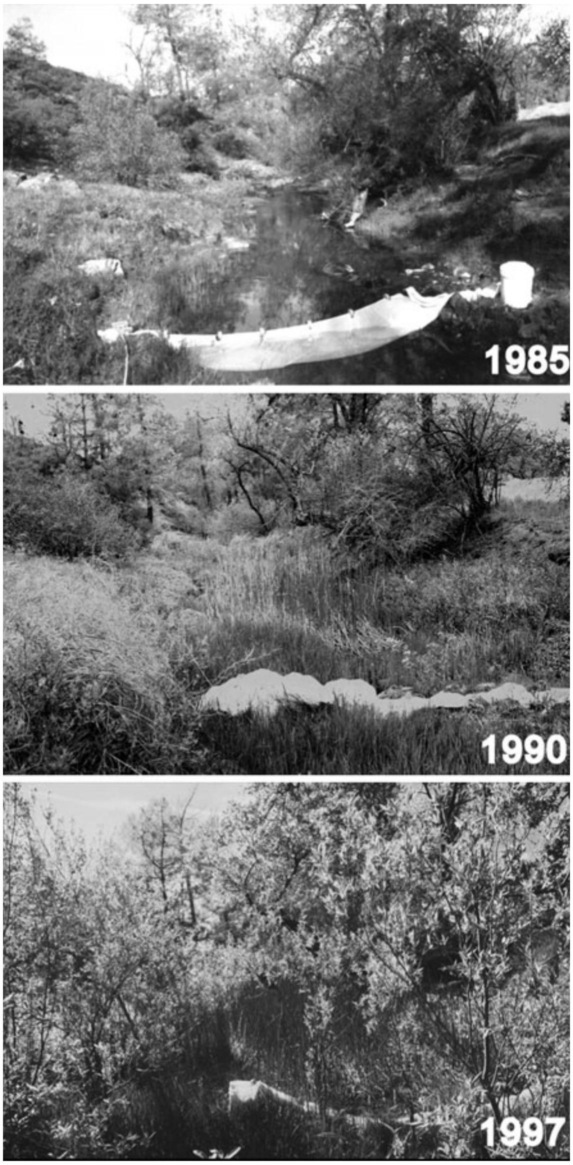

Fig. 5 Instream aquatic vegetation at a first-order HC site before (1985), during (1990), and after (1997) a prolonged drought. Similar photographs were taken annually at each site and used to qualitatively assess vegetation changes

(e.g., Gasith & Resh, 1999). In terms of the competition and predation between native roach and non-native green sunfish, once normal to wet conditions began to prevail post-drought, roach abundance increased and size distributions returned to pre-drought conditions, indicating recovery of not only abundance but also size structure. In contrast, when habitat contracts as during a prolonged drought period, both displacement and predation by green sunfish could have reduced roach abundance, recruitment, and survival (Moyle, 2002; Moyle et al., 2003), as evidenced by the shift in size distribution to mostly large individuals during those periods. Alternatively, when habitat diversity is high (i.e., riffles and pools are abundant), as it occurs during average and wet rainfall years, competitive displacement and high predation result in habitat segregation, with roach being displaced to riffles and other shallow habitats. However, in the absence of green sunfish, roach are almost always present in pool habitats (Moyle, 2002).

Droughts can decrease macroinvertebrate population fitness

In med-climate streams, life cycles of benthic macroinvertebrates are closely tied to within-year cycles of flooding and drying (Gasith & Resh, 1999). In BSC, Lamberti and Resh (1983) demonstrated that exploitative, interspecific competition occurred in early instars of the caddisfly *Helicopsyche borealis* in a 3rd-order coastal California stream. They demonstrated that this competition resulted from high survival of larvae that occurs during the dry season. However, numbers of early instars of this species are typically reduced by wet season rains and consequent flooding; therefore, intraspecific competition ceases as a result of flood-induced larval mortality.

In a subsequent field experiment, Feminella and Resh (1990) demonstrated the influence of this med-stream's hydrologic regime on competition potentially occurring over the course of the life cycle of *H. borealis*. Densities of this species were manipulated experimentally to reflect those that would occur under wet-year, dry-year, and harsh-drought conditions. These experimental densities were determined using long-term data from multi-year surveys under different annual flow regimes that revealed a relationship between wet-season hydrologic regime and subsequent densities of *H. borealis* (Resh et al., 1984). In wet and normal rainfall years, floods reduced late-instar densities to levels below which intraspecific competition would occur. However, in drought years, densities were not reduced by floods and intraspecific competition continued through emergence and into the adult stage (Feminella & Resh, 1990). This competition actually reduced fecundity in the adult stage and consequently overall population fitness of *H. borealis*.

The above study demonstrates that hydrologic conditions can have population-level consequences. Following this demonstration, Feminella and Resh (1990) examined a 138-year precipitation record to determine how often conditions under which severe drought, and consequently a population fitness reduction, would occur in this population of *H. borealis*. Using the severe drought year as a benchmark of density-dependent population regulation, they found that severe drought conditions would have occurred during about 4% of the years. Therefore, although density-dependent factors may be important during the dry season when pools form and biotic interactions such as predation and competition increase in importance (Gasith & Resh, 1999; Power et al., 2008), Feminella and Resh's (1990) study, conducted during the wet season, demonstrates the importance of density independent factors during most (96%) years. In light of predictions regarding climate change in California's med-climate region (Lawrence et al., 2010), and the demonstration that hydrologic conditions may have population-level effects, such reductions in population fitness may become more frequent in the future and perhaps act as a selective force in these streams.

Community-level studies

Alteration of stable states of ecosystems following drought influence macroinvertebrates and fishes

Drought may affect community resilience over time, and may do so through changes in habitat. For example, Bêche et al. (2009) examined the ability of macroinvertebrates and fishes to return to a reference state following prolonged drought, using 20 years of data collected at HC and KC. This period included a 5-year drought and several years of above-average annual precipitation. The reduction in flow and connectivity during the extended drought resulted in a lower mean-substrate size and allowed aquatic and riparian macrophytes (e.g., *Typha*, *Carex*, *Eliocharis*, *Salix*, and *Scirpus*) to increase in density, thus reducing the volume and area of aquatic habitat (Fig. 5). Even following normal rainfall years, much of this vegetation still remained rooted in the smaller streams. Although macroinvertebrate taxa richness in the above streams recovered rapidly post-drought, persistent changes in community composition were evident among pre-drought, drought, and post-drought years. Moreover, the drought resulted in a directional change in community composition with no clear recovery to pre-drought conditions, even following the return of wet-year flows.

Drought can result in a shift to communities with different biological traits. For example, Lawrence et al. (2010) found significant biological trait responses (e.g., a decline in large, long-lived organisms) that were related to long-term temperature increases and precipitation decreases in these small streams. Other studies have demonstrated that droughts can have equivalent effects on the structure of macroinvertebrate communities (Dewson et al., 2007). However, considerable change in the taxonomic and trait composition of communities may occur even if community structure remains unchanged (Bêche & Resh, 2007b; Bêche et al., 2009).

The studies at HC described above demonstrate that irreversible "regime shifts," a change from one relatively stable community state to another (i.e., alternative stable states, Scheffer et al., 2001), in local communities may occur as a result of long-term press (or continuing) disturbances to the flow regime (Lake, 2003), such as a multi-year drought (Bêche et al., 2009). Regime shifts usually result from abiotic disturbance and have been described as "catastrophic" when the return to pre-disturbance conditions (in this case, flow) does not result in community recovery (Scheffer et al., 2001). In HC and KC, Bêche and Resh (2007a, b) and Bêche et al. (2009) reported that prolonged drought resulted in directional change in community composition in both streams, and that there was no evidence of macroinvertebrate "recovery" from drought (i.e., no return to a pre-drought community composition).

Although the fish community in these streams only contained three native and one non-native species, native fish abundance was the lowest during the drought years and the highest during the following wet years (see also Marchetti & Moyle, 2001; Bernardo et al., 2003). At a non-perennial site examined in HC, where the dense vegetation that formed during the multi-year drought was highly resilient to even dramatic increases in flow, a parallel decline in the numerically dominant California roach population was observed. In fact, the change in vegetation has transformed this site from one with a perennial flow regime to one with a non-perennial flow regime, and amounts of in-stream vegetation continues to increase in density and cover (Fig. 5). Thus, a positive feedback between flow and habitat conditions was created in which flow was reduced because of high density of aquatic macrophytes, which in turn favor the continued spread of these macrophytes by increased siltation and dominance of shallow habitat. This flood-resistant habitat may represent an alternative stable state that resulted from the multi-year drought disturbance that in turn resulted in a permanent regime shift in the local macroinvertebrate community and displacement of fishes (Bêche & Resh, 2007a, b).

Alternative stable states are expected to be more common in systems with strong underlying abiotic regimes (Didham & Watts, 2005), such as streams (Resh et al., 1988), and especially for streams in med-climates (Gasith & Resh, 1999). Examples of such alternative stable states in stream ecosystems include restoration efforts that failed to result in "recovery" in community composition (Didham & Watts, 2005). In the case of the non-perennial site examined in HC, a press disturbance altered the physical and biological habitat of macroinvertebrates and fishes, and this altered state has proven resistant over the course of many years to the "restoration" of winter floods. A recent study in a desert Southwest stream has equally demonstrated regime shifts in macroinvertebrate communities as a result of multi-year drought (Bogan & Lytle, 2011). They proposed a conceptual model of temporal community changes demonstrating how press disturbances, such as multi-year droughts, can create alternative stable states that are reinforced by altered abiotic and biotic pressures, whereas pulse (or intermittent) disturbances and seasonal fluctuations will ultimately result in recovery to the original community state.

Seasonal variability can be influenced by annual variability

Seasonality in the composition of stream macroinvertebrate communities likely occurs to some extent in all climate regions but it is more pronounced as the seasonality of flow or other factors become more pronounced within a year. Med-climate streams are extreme examples of seasonality because they are characterized by annual, distinct wet and dry seasons, where sequential patterns of flooding and drying occur each year (Gasith & Resh, 1999). From year to year, the occurrence of the wet season is predictable but the magnitude of the flooding is not (Resh et al., 1988). Arguably, the sequential pattern of flooding followed by drying creates the harshest conditions for benthic macroinvertebrates and fishes found in any freshwater environment.

Research in med-climate streams in California (e.g., Cooper et al., 1986; McElravy et al., 1989) and other med-regions (e.g., Pires et al., 2000; Bonada, 2003) have clearly demonstrated the presence of distinct wet- and dry-season macroinvertebrate taxa. Moreover, seasonal differences in the trait composition of macroinvertebrates in mediterranean streams (med-streams) may differ as well. In studies of HC and BSC, Bêche et al. (2006) examined trait composition in non-perennial (HC) and perennial (BSC) streams and found that they were similar to each other in overall faunal composition and structure. However, the wet- and dry-season communities were relatively discrete taxonomically, as was their density and species diversity values (Bêche et al., 2006). Moreover, there was greater variation in trait composition during the dry season than during the wet season over the 20-years period examined.

Seasonal differences in biological traits of the macroinvertebrate community were greater in the non-perennial stream (HC) than in the perennial stream (BSC) and, over multi-year periods, traits varied seasonally much less in the perennial stream than in the non-perennial one (Bêche et al., 2006). In fact, dry-season trait composition of BSC was more similar to the wet-season trait composition of HC than the dry-season trait composition of BSC. When trends were examined over multiple years, seasonal differences were noted in both trait and taxonomic composition. Differences, however, decreased with decreasing total rainfall (i.e., wet-season communities became more like dry-season communities as rainfall decreased) and, with lower rainfall, differences were more pronounced in the non-perennial stream.

Environmental factors can produce both intra- and interannual differences in amounts and types of available habitat. Bêche et al. (2006) reported that habitat variability was the highest in the non-perennial stream in the dry season (ranging from a dry stream bed to a flowing stream) but the highest in the perennial stream in the wet season. Likewise, the non-perennial stream sites at HC exhibited more variability in trait composition across years in dry than in wet seasons. Similar results have been found in Spanish med-climate streams (Rieradevall et al., 1999; Bonada et al., 2007). In contrast, the perennial stream at BSC exhibited more variability across years in wet than in dry seasons.

Seasonal changes also occur in the hyporheic zone. This habitat may represent an important source of colonists following wet-season floods. In a med-climate stream in California, McElravy and Resh (1991) found that richness and abundance of benthic macroinvertebrates in the 0–0.5 cm surface layer declined during the wet season but remained the same or higher, respectively, than that found in deeper layers (5.1–35 cm). However, seasonal faunal differences within these below-surface layers were less than differences found at the surface, presumably because substrate disturbances from floods are less pronounced below the surface. Most studies of the hyporheic fauna have been done in temperate regions (e.g., Franken et al., 2001; Storey & Williams, 2004) where less seasonality is apparent than in med-climate regions. Although long-term hyporheic data are lacking in med-climate streams, McElravy and Resh's (1991) study period was done in above-average precipitation years that included a 100-year flood, and the seasonal stability observed in the lower substrate zones is remarkable and may provide continuity of recolonists.

Similarly, fish communities in med-regions often show marked seasonality in patterns of abundance and density (e.g., Pires et al., 1999), which in California med-streams is at least partly attributable to variation in the timing of reproduction. Many of the native fishes spawn in the spring during periods of high flow (typically February–April), whereas many of the non-natives spawn in the summer (Moyle, 2002). Differences in the timing of reproduction alone can lead to pronounced shifts in the relative abundance of natives and non-natives across the summer drought season. For example, in a study of the larval fishes of lower PC, Marchetti and Moyle (2000) found that larvae and juveniles of native fishes occurred much earlier in the year (March through early June) than the larvae and juveniles of non-native fishes (June through August). However, biotic interactions can greatly alter recruitment to larger size classes because the smallest individuals are the most susceptible to predation by gape-limited piscivores, such as non-native green sunfish predation on native larval roach, which can reduce the abundance of the latter species.

Research in a Portuguese med-stream has also revealed the importance of timing of reproduction relative to environmental variability in explaining seasonal and interannual variation in fish population dynamics. Magalhães et al. (2003) report that native nase (*Chondrostoma lusitancicum*) spawned early in the year (January–April) and that variation in their dynamics was partly the result of the magnitude of spring floods, with density of age-2 nase decreasing following a severe flood. In contrast, since the native chub (*Squalius torgalensis*) spawned later in the year (March–June), their dynamics were relatively more influenced by the severity of summer drought, and consequently density of age-1 chub decreased following a severe drought (Magalhães et al., 2003).

Similar to research in med-streams in California (Bêche et al., 2009), predation in Portuguese med-streams can be an important factor influencing seasonal variation in fish communities. For example, studies in the Guadiana basin in Portugal suggests that predation by non-native pike (*Esox lucius*) might be responsible for the large reduction, from spring to summer, in native fish abundance at one sampling site, where the non-native pike were abundant. Together, this research from Portugal and California med-streams suggests that seasonal shifts in fish assemblages may be strongly influenced by interannual variation in both biotic (e.g., predation) and abiotic (e.g., timing of precipitation) factors.

Short-term climatic trends result in shifts in fish communities

Short-term climate trends can drive fish community shifts, just as they can for benthic macroinvertebrates in med-climate streams. Marchetti and Moyle (2001) documented shifts in the fish community of lower PC from 1994 to 1998. PC is a regulated system with flow regime being strongly influenced by water diversions except during winters of high precipitation. Fortuitously, their study period coincided with a series of extremely dry years (1994, 1995) that was followed by a series of extremely wet years (1997,1998), which allowed examination of shifts in the lower creek fish communities under different flows. In general, the non-native fishes were favored in dry years that lacked peak spring flows, which apparently flushed these fishes from the system. In contrast, the native fishes were favored during wet years, when high winter and spring flows created conditions that were favorable for spawning and rearing by native fishes. The reduction in abundance of non-natives during the wet years combined with several strong recruitment years for the natives led to a dramatic shift in the fish community over the course of the study, from one dominated by non-natives to one dominated by natives (Marchetti & Moyle, 2001). These results highlight the importance of elevated spring flows for native fish reproduction, and also indicated that restoration of a more natural flow regime that captured elements of the strong seasonality characteristic of med-climate streams would benefit native over non-native fishes. A similar result was reported in the Guadiana basin in Portugal (Bernardo et al., 2003). Moreover, researchers have also shown similar results in the Torgal catchment of south-west Portugal, but with a focus on shifts in the relative abundance of different native species that differ in their timing of spawning and reproductive investment (Magalhães et al., 2003, 2007).

In general, many native fishes in California are long-lived and iteroparous (Moyle, 2002), with high adult survival but low reproductive success in any given year, especially during drought years. Their longevity allows them to persist through short-term droughts and to reproduce during wetter years with more favorable spawning and rearing conditions (Marchetti & Moyle, 2001). This combination of traits (i.e., spring spawning, long-lived, high adult survivorship) is also found in two common med-stream fishes in the Mediterranean Basin (*Squalius torgalensis* and *Chondrostoma lusitanicum*, Magalhães et al., 2003), and may represent adaptations that increase the likelihood that native fishes will encounter at least 1 year with conditions that are suitable for reproduction in med-climate regions. In California, where non-native fishes are widespread, the fish community may shift toward a higher representation of non-natives when short-term climate trends do not favor reproduction for natives.

Med-climate stream management studies and implications

Biological-monitoring metrics that have low seasonal variation have broader temporal applicability

Depending on the magnitude, timing, and duration of precipitation and consequent flows, the continuation of the wet-season community into the dry season may be extended or reduced in med-climate streams (Gasith & Resh, 1999; Bêche et al., 2006). Therefore, useful bioassessment metrics should either show stability in values that are independent of season or be restricted in their application to the season in which temporal variability is minimal.

Biological metrics would be expected to vary greatly in their response to seasonal differences in highly seasonal environments, like in med-climate regions (Resh & Jackson, 1993; Resh, 1994). Seasonal variability in benthic-macroinvertebrate communities arises from both physical (e.g., reduced flow, lower oxygen concentrations; Gasith & Resh, 1999) and biological (e.g., predation and competition; Power et al., 1988; Power et al., 2008) factors that may alter community composition. In order to test the applicability of this expectation for California med-streams, Mazor et al. (2009) examined the components of the North Coastal California Index of Biological Integrity (Rehn et al., 2005), which included metrics based on richness and taxa composition, and also the ratio of observed to expected taxa (O/E) used in the California RIVPACS model (Ode et al., 2008). Analysis of 20 years of collections in HC and KC for 66 metrics (Table 2) indicated that some of the metrics (e.g., % GOLD, i.e., Gastropoda, Oligochaeta, and Diptera, or total richness) showed low seasonal variability but others had very high variability. High-variability metrics would not be useful for distinguishing the effects of natural and human-caused disturbances. Variability in traits-based metrics was higher than other metrics, and aggregation of metrics into a multi-metric index reduced variability. Metrics with low seasonal variability represent characteristics of macroinvertebrate communities that are relatively resistant to these physical and biological events that occur within a season, and thus represent more useful metrics for biological monitoring in med-streams.

However, seasonal variability does not operate independently of either annual variability or spatial variability for biological-monitoring metrics. Seasonal variability may be influenced by annual variability in, for example, emergence times, and hastened or prolonged changes in flow and water chemistry (Jackson & Füreder, 2006; Gallo et al., 2010). Smaller streams may be affected more by interactions of seasonal variability and annual variability because of the disproportional influences of droughts as a result of the lower total volume of water (e.g., Rosenberg & Resh, 1993).

Table 2 Seasonal and annual variability for metrics examined

Metric	Seasonal variability			Annual variability		
	Mean CV	Std. Dev.	Range	Mean CV	Std. Dev.	Range
Abundance						
Total no. individuals	14	9	0–30	14	4	10–19
No. Ephemeroptera	52	34	3–141	26	10	17–39
No. Plecoptera	139	9	104–141	54	9	45–66
No. Trichoptera	53	34	2–114	42	16	25–59
No. EPT	40	31	3–131	18	3	14–21
No. Chironomidae	28	17	3–54	26	9	16–38
No. Diptera	19	13	0–36	22	7	17–33
No. Baetidae	89	54	0–141	36	11	26–52
No. Hydropsychidae	141	0	141–141	154	100	76–300
No. Odonata	107	27	46–141	123	51	81–195
No. Coleoptera	68	50	4–141	70	10	56–78
No. non-insects	38	15	16–68	49	22	33–82
No. OCH	63	34	0–128	62	13	49–79
No. GOLD	16	12	1–34	21	8	17–33
Composition						
% Ephemeroptera	101	40	9–141	62	30	34–104
% Plecoptera	141	1	136–141	93	15	73–106
% Trichoptera	91	42	4–137	82	32	46–119
% EPT	104	33	8–136	46	24	14–71
% Chironomidae	60	47	1–132	55	14	35–66
EPT/EPTC	98	32	9–134	43	24	12–69
% Diptera	50	44	0–128	33	13	16–45
Chironomidae/Diptera	32	25	2–105	32	6	25–39
Baetidae/Ephemeroptera	80	63	0–141	33	5	28–37
Hydropsychidae/Trichoptera	141	0	141–141	164	104	94–318
% Odonata	125	17	91–141	145	47	99–203
% Coleoptera	84	46	7–141	97	24	70–123
% non-insects	67	37	4–126	72	19	52–94
% OCH	82	33	26–134	85	17	67–108
% GOLD	41	37	4–107	31	14	16–45
Diversity						
Species/genus level						
Shannon–Wiener diversity	20	15	1–49	15	3	12–19
Margalef's diversity	18	13	0–39	20	4	16–26
Evenness	20	14	2–50	13	2	11–16
Simpson's diversity	16	14	0–41	10	3	7–15
Richness	20	14	1–60	27	8	21–39
Ephemeroptera richness	45	36	0–141	30	15	15–43
Plecoptera richness	138	12	90–141	49	10	40–62
Trichoptera richness	49	34	6–116	46	18	31–68
EPT richness	54	31	17–132	29	7	21–35
Chironomidae richness	27	19	0–65	26	6	21–35

Table 2 continued

Metric	Seasonal variability			Annual variability		
	Mean CV	Std. Dev.	Range	Mean CV	Std. Dev.	Range
Diptera richness	28	18	0–59	25	9	20–38
Odonata richness	103	31	31–141	107	38	58–151
Coleoptera richness	75	44	6–141	69	6	62–76
Non-insect richness	40	23	0–80	53	19	43–81
OCH richness	54	39	2–131	68	12	53–83
GOLD richness	23	15	1–44	25	9	19–39
Family level						
Shannon-Wiener diversity	21	20	2–69	23	8	12–29
Margalef's diversity	14	10	0–31	21	5	16–26
Evenness	24	20	1–70	22	8	11–30
Simpson's diversity	22	24	1–78	21	10	7–30
Richness	18	15	3–53	25	6	20–34
Ephemeroptera richness	45	36	0–141	30	14	15–43
Plecoptera richness	138	14	85–141	45	10	36–57
Trichoptera richness	43	33	8–106	43	16	27–60
EPT richness	48	33	4–129	28	8	20–37
Diptera richness	29	22	3–80	19	6	15–27
Odonata richness	100	34	31–141	97	33	54–129
Coleoptera richness	66	48	18–141	61	8	51–71
Non-insect richness	40	23	0–80	53	19	43–81
OCH richness	59	37	0–131	59	8	48–66
GOLD richness	19	14	0–47	22	7	16–31
% dominance (1 taxon)	18	15	0–51	26	7	18–35
% dominance (2 taxa)	11	7	2–24	15	3	11–18
% dominance (3 taxa)	7	4	1–13	10	1	10–11
% dominance (4 taxa)	4	3	0–10	7	1	7–8
% dominance (5 taxa)	2	2	0–7	5	1	4–7
Traits						
Species/genus level						
CTV	11	9	1–26	9	3	6–12
% tolerant (CTV >7)	111	27	57–139	130	44	96–194
% intolerant (CTV <3)	115	38	32–141	73	13	60–88
% <1 gen/years	66	29	7–127	90	22	70–120
% 1 gen/years	17	17	0–56	15	6	7–21
% >1 gen/years	10	8	0–23	12	5	5–17
% gill or cutaneous respiration	7	5	0–13	6	3	3–11
% air breathing	58	42	0–119	52	13	35–67
% crawlers	11	10	2–29	8	2	5–9
% predators	37	28	9–97	32	4	27–36
% shredders	23	18	0–59	35	1	34–36
% scrapers	32	26	0–103	22	8	11–31
% filterers	67	41	8–133	59	10	44–67
Scrapers/(scrapers + filterers)	19	17	1–69	16	4	12–20

Table 2 continued

Metric	Seasonal variability			Annual variability		
	Mean CV	Std. Dev.	Range	Mean CV	Std. Dev.	Range
Family level						
CTV	10	8	1–25	8	3	6–12
% tolerant (CTV >7)	115	24	70–141	122	44	95–188
% intolerant (CTV <3)	122	32	47–141	75	14	61–87
% <1 gen/years	62	31	13–117	84	18	70–109
% 1 gen/years	16	14	1–50	18	6	12–26
% >1 gen/years	9	6	1–20	11	3	8–14
% gill or cutaneous respiration	7	5	0–30	6	3	3–11
% air breathing	58	42	0–119	52	13	36–68
% crawlers	10	9	0–27	8	2	5–9
% predators	36	29	1–94	30	3	27–33
% shredders	25	19	4–63	36	1	34–37
% scrapers	32	23	3–98	22	8	10–28
% filterers	67	41	8–133	59	10	44–67
Scrapers/(scrapers + filterers)	19	17	0–69	16	4	13–21
Multivariate						
O/E100	20	13	3–57	27	8	21–39
O/E50	14	14	1–56	16	5	12–23
Family						
O/E100	18	14	7–57	25	6	20–34
O/E50	11	15	0–65	14	1	14–15

Seasonal variability was calculated as the Coefficient of Variation (CV) of the spring and summer means for each year at the first-order, perennial site at HC. SD is the Standard Deviation. Annual variability was calculated as the CV of the mean values of each year for each site. EPT represents the benthic macroinvertebrate orders Ephemeroptera, Plecoptera, and Trichoptera. OCH represents the orders Odonata, Coleoptera, and Hemiptera. GOLD represents the orders Gastropoda, Oligochaeta, and Diptera. California tolerance values (CTV) represent the tolerance on a scale of 0 (very intolerant) to 10 (very tolerant) of benthic taxa local to the state of California to pollution. O/E represents the ratio of taxa observed to those expected statistically based on their presence at all reference sites, i.e., O/E(100), or 50% of reference sites, i.e., O/E(50)

Moreover, variance components analysis of long-term HC and KC metrics similarly showed that annual variability was generally larger than seasonal variability (Mazor et al., 2009).

Whether a stream has perennial or non-perennial flow is related to magnitude, timing, and duration of precipitation events during the wet season in med-climate regions. Lunde (2011) recently emphasized the need to develop both unique biomonitoing metrics and composite indices of biological integrity (IBIs) for non-perennial streams in the med-climate of California. IBIs have been developed using benthic macroinvertebrate data from perennial streams there, but their applicability to non-perennial streams even within their development region was unknown. When either the Southern Coastal California IBI (Ode et al., 2005) or the Northern Coastal California IBI (Rehn et al., 2005) was applied to non-perennial streams, the scores were consistently lower than in perennial streams (Lunde, 2011). Non-perennial streams support unique biological communities in med-climate Californa, which is likely the case in all med-climate streams (Gasith & Resh, 1999; Morais et al. 2004; Bonada et al., 2006). Therefore, the need for development of specific indices for non-perennial systems should not be surprising and needs to be addressed in the future.

The high annual variability of many biological-monitoring metrics may limit their usefulness

The presumption underlying all biological-monitoring studies is that variability in communities caused by human disturbance can be distinguished from natural variability through the establishment of appropriate biological expectations, most commonly through analysis of reference conditions (Resh et al., 1995; Gebler, 2004; Bonada et al., 2006). However, the level of annual variability in commonly used metrics has not been well evaluated in most monitoring programs, and high annual variability may pose a major challenge in using metrics to accurately determine ecological condition (Jackson & Füreder, 2006). Metrics with low annual variability under un-impacted conditions, as well as high responsiveness to human disturbance, will be most useful for detecting anthropogenic influences.

High annual variability may increase both Type I and Type II errors, for example, by obscuring human impacts or, conversely, by indicating deteriorating quality when conditions actually fall within the range of natural variability for these metrics. Other studies have shown the importance of considering long-term, annual variability of biological-monitoring data (e.g., Scarsbrook et al., 2000). Unfortunately, many bioassessment programs typically use 3–4 years of collections for index development or model calibration (Mazor et al., 2009). We believe that more detailed evaluation of the amount of annual variability in various biological-monitoring metrics is a critical, and much needed, future step toward identifying useful biological-monitoring metrics in med-climate systems.

The amount of annual variability detected is strongly influenced by the type of metric used in the analysis (Table 2). For example, based on studies in a California med-climate stream (Mazor et al., 2009), most abundance and composition metric-types are much more variable than diversity and richness, traits-based, and multivariate metrics. However, a few metrics based on specific, often uncommon, taxa (e.g., Plecoptera richness) and some species traits (e.g., % tolerant taxa) had high average annual variability.

Biological-monitoring programs can choose among different, temporal windows-of-reference periods

A major challenge for ongoing biological-monitoring programs is to determine an appropriate method for using historic data to create reference periods. Reference periods are the annual equivalent of spatially defined reference conditions, with years being the unit of replication rather than sites (Reynoldson et al., 1997; Bailey et al., 2003). Using the long-term HC and KC data, Mazor (2006) evaluated the precision and accuracy of three approaches for creating reference periods, which he defined as moving windows, growing windows, and rainfall-based reference periods (Fig. 6). In the (A) moving-windows approach, a fixed number of years before the test year were used to establish the reference period. The reference condition was recalibrated each year as new data were available, and older data were ignored. In the (B) growing-windows approach, all years before the test year were used to establish the reference period. The reference condition was recalibrated each year as new data were available, and old data were retained. In the (C) rainfall-based approach, only years with rainfall regimes similar to the test year were used to establish the reference condition and all other years were ignored. All reference conditions were defined for individual sites, in contrast to the traditional applications of the reference-condition approach in which reference conditions are defined for a region with similar topographic, geological, and hydrological characteristics.

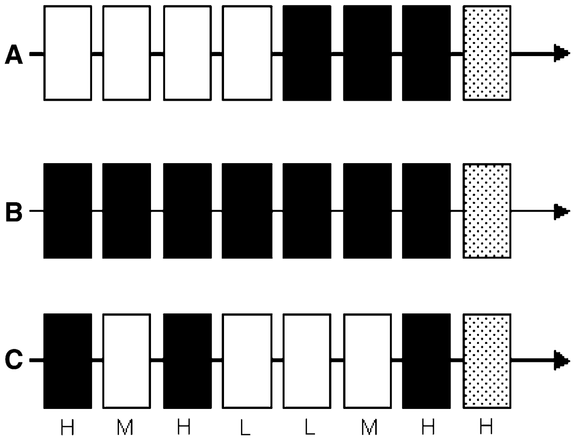

Fig. 6 Three approaches to establishing reference periods with long-term data: **A** moving window, **B** growing window, and **C** rainfall-based. Each rectangle represents a year of biological data, and arrows indicate the passage of time. *Black squares* represent years used to establish the reference period, *gray squares* represent the test year, and *white squares* represent years that are not considered using the different approaches. H symbolizes years with high rainfall, M years with moderate rainfall, and L years with low rainfall

Creation of appropriate reference periods can be based on the precision and bias of biological assessment metrics used. Precise reference periods result in predictions of metric values that are close to observed values, and depend on site and season. Biased reference periods result in predictions of metric values that are frequently greater than or less than observed values. Mazor (2006) found that precision was the highest with large moving windows (i.e., reference periods that included a large number of years) or with rainfall-based reference periods, and intermediate to poor with growing-window reference periods. At all sites and seasons, larger moving windows were more biased than expected. Rainfall-based reference periods had large bias as well (Fig. 6C). With few exceptions, all reference periods produced negative bias for most metrics examined.

Although using a large number of years of data improves precision, the inclusion of older data can bias predictions of future biological conditions. At all sites and seasons, large moving-window reference periods were highly biased for most metrics examined. Moving windows of about 6 years produced more precise and less biased biological assessments than other reference-period approaches and reference-window lengths. For most metrics examined, approaches based on maximizing data (i.e., the growing-window approach) did not provide consistently precise and unbiased predictions. Short-term antecedent events (e.g., recent floods or low flows) were found to have greater influence than longer term antecedent conditions. Sensitivity assessments are important to consider for reducing bias to better assure that biological impairment can be detected by the reference period used (e.g., Carlisle & Clements, 1999). Long-term data are essential to do this in an appropriate manner.

Long-term data can be used to monitor and exclude climate-change effects

Climate change is expected to have strong, long-term effects on temperature and precipitation regimes in med-climate regions worldwide, including increasing temperatures, decreasing precipitation, more extreme flood and drought events, and changes in the timing and duration of the rainy season (IPCC, 2008). Climate-change scenarios in different med-climate regions, the anticipated effects on freshwater biota in these regions, and the concerns for conservation are discussed in Filipe et al. (2012). Water-resource managers in med-climate regions will need to monitor climate-change effects and to separate these from confounding factors related to human disturbance that affect aquatic ecosystems. Therefore, it is important to both develop metrics that are responsive to climate-change effects and, concurrently, to determine which metrics are unresponsive to climate-change effects while being responsive to the effects of human disturbance that are important to water-resource managers. The latter is critical in terms of using existing past data for comparisons.

Strong correlations have been found between several biological assessment metrics and a set of climatic variables, including mean summer temperature and the El Niño Southern Oscillation Index, based on the KC and HC datasets (Mazor et al., 2009). Lawrence et al. (2010) extended this analysis and used a combination of both daily rainfall and degree-day analysis to create reference periods from historic data to analyze the effects of climate change on these benthic communities. In this approach, benthic-macroinvertebrate communities are predicted to become less like those observed in cool, wet years and more like those observed in warm, dry years as a result of directional changes in precipitation and temperature patterns that are anticipated with climate change in California. Lawrence et al. (2010) then analyzed the sensitivity of common biological-monitoring metrics for detecting the effects of climate change, developed a climate-change indicator specifically for this purpose, and also examined responses in a set of a priori-selected traits to climate-change effects.

Although this study found that the common metrics used in biological monitoring will continue to have applicability in biological assessment programs under changing climate conditions, these metrics are based mostly on low taxonomic resolution. Thus, significant replacements in taxa composition could be occurring in the community at the genus and species levels that these metrics would fail to detect, which is a problem well documented in biomonitoring (Lenat & Resh, 2001). The inclusion of a traits-based approach provides a more comprehensive way of evaluating the potential effects of climate change in these marginal environments.

Most macroinvertebrates collected in long-term, med-climate stream studies are temporally rare

In ecological surveys, rare species can include those that are either temporally or spatially uncommon (or both), and this designation often has conservation, monitoring, and management implications. The lack of consistent long-term data from streams has resulted in a paucity of information on the temporal rarity of most freshwater taxa, especially benthic macroinvertebrates. Resh et al. (2005) examined the frequency of occurrence of macroinvertebrates at four sites in HC and KC based on 19–20 years of collections and compared these to two shorter, 7-year (BF) and 8-year (BSC), datasets from other California med-regions. In all streams examined by Resh et al. (2005), a large proportion of the taxa (17–33%) occurred in only 1 year of the long-term sampling. In general, the temporal frequency of occurrence increased as population density increased, and rare species tended to have low densities in the single year that they were collected. Likewise, only a small percentage (<11%) of the taxa were found in all years of the long-term studies. Temporally rare and temporally common taxa showed different biological traits that may explain their occurrence. For example, common taxa had shorter life cycles with multiple generations, whereas rarer taxa had poor dispersal abilities.

Temporal rarity can result from a variety of factors operating at different scales, such as shifts in species distribution with climate change (Walther et al., 2002) and logistic problems such as sampling inconsistency by operators or changes in sampling methods used (Hannaford & Resh, 1995; Hannaford et al., 1997). Differences in microhabitats sampled or shifts in microhabitats occupied by the species may also influence temporal occurrence.

Although there are no long-term med-region datasets currently available that we could find for comparison, Resh et al. (2005) did compare their results with a macroinvertebrate dataset available from a Netherlands stream (Pillot, 2003) and found a similar pattern where temporally rare species predominated in collections. In addition, when a study in a med-climate region of western Australia was compared macroinvertebrate data collected in 2006 and 2007 with an earlier study in the same streams (Doeg, 1996), each year's taxa were distinct (Chester & Robson, 2011). A review of temporal rarity by Magurran (2007) indicates that this phenomenon of the common occurrence of temporally rare species is observed in a wide range of ecosystems and for many different community types (e.g., estuarine fishes, forest hymenoptera, and birds). Furthermore, she highlights the parallels between temporal and spatial patterns of occurrence and abundance, whereby communities are composed of a small core of common and abundant taxa (across space and time) and a large group of rare taxa with low abundance. Therefore, this temporal rarity is not likely to be a phenomenon that applies only to med-climate streams but rather a more general pattern that may apply to streams in all regions of the world. Additional research (long-term datasets, as well as meta-analyses of existing data) are needed to confirm this hypothesis and to develop plausible mechanisms to explain temporal rarity of macroinvertebrate taxa in streams.

Long-term information is needed to monitor invasive species

The composition and abundance of native fauna in freshwater streams in med-climate regions (and often elsewhere) can be greatly influenced by the presence of non-native invasive species, as has been demonstrated above for fish communities in HC and PC. Moreover, non-native species themselves may result in economic as well as ecological damage. The Chinese mitten crab *Eriocheir sinensis*, a catadromous crab from coastal Asia that lives in freshwater streams and moves downstream into estuaries to reproduce, was first found in SFBA in the early 1990s. The ecological and economic impacts of this invasive species include their potential impacts on freshwater and estuarine food webs during periods of high abundance, their interference with California's agricultural water supply system during mass downstream-migration events, and their potential to threaten levee stability because of their burrowing behavior (Rudnick et al., 2000, 2005; Rudnick & Resh 2005). *E. sinensis* showed rapid population increases throughout the 1990s and early 2000s (Rudnick et al., 2000, 2003). For example, in 1992, they were restricted to streams in the south part of San Francisco Bay. By 1994, however, they were found in the immediate tributaries to the main body of the Bay. In 1996, they were distributed throughout the central and western part of the San Francisco Bay Delta and South Bay tributaries, and by 1998 they had expanded to the Sacramento and San Joaquin Rivers and their tributaries. At this time, their distribution included several hundred km^{2}of freshwater and estuarine habitats, making it one of the most widely spread aquatic invasive species in the western United States (Rudnick et al., 2000, 2003).

By the mid-2000s, however, the *E. sinensis* population in SFBA was in a steep decline (Hieb, 2009). By 2009–2010, no crabs were collected in the numerous, detailed surveys conducted in the previously known habitats (Hieb, 2010). The reasons for this sudden decline are not well understood. However, these crabs have a lower threshold for temperature tolerance in their larval development, and low temperatures have been shown to be correlated with smaller larval cohorts of this species in SFBA (Blumenshine et al., 2012). Therefore, low winter temperatures coincident with the appearance of early-stage larvae may be a factor in the decline of this species.

Long-term monitoring of this invasive species was critical in terms of the implementation of costly economic decisions related to control efforts and levee modification. Surveys to determine its distribution along with correlations with climate factors that are particularly important in med-climate regions provided both documentation of the population dynamics of this invasive species and a mechanism to explain their decline in the event of their reappearance.

Restoration monitoring may require long periods before stability occurs

Stream restoration projects in med-climate streams are increasingly common (see Kondolf et al., 2012), but consistent post-project monitoring of whether projects achieve established goals is rare (Kondolf & Mitchell, 1995; Bernhardt et al., 2005). Inadequate funding for post-project monitoring or fears of failure by project managers have been identified as deterrents to the evaluation of completed restoration projects (Kondolf, 1995). Clearly, this lack of monitoring and evaluation impedes the field of restoration science because future restoration projects cannot glean knowledge from the performance of past projects (Kondolf, 1998). This is especially true for small-scale projects, such as that examined by Purcell et al. (2002) in an initial evaluation of how a 70-m reach of Baxter Creek (BC) located in a small urban park responded to restoration efforts. Restoration efforts involved opening a previously culverted channel, planting riparian vegetation, and adding step-pool sequences and sinuosity. Biological condition, as measured by benthic macroinvertebrates, was higher in the restored reach of BC compared to unrestored sections within the same watershed, but was below that of a nearby control stream, which was restored 12 years earlier (Purcell et al., 2002).

Periodic evaluations of habitat condition at the restored reach (BC) using a visual-based habitat assessment (Barbour et al., 1999) indicated that habitat condition improved steadily over the 7-year period following the initial assessment. These habitat improvements occurred primarily because of increased bank stability and decreased sediment deposition at the restoration site. Geomorphic surveys completed in 1996 and 2005 also revealed an increase in the number of step pools over time at the restored site that presumably increased habitat complexity for benthic macroinvertebrates (Chin et al., 2009). In contrast, habitat assessment scores of an unrestored BC site and previously restored site (Strawberry Creek, Charbonneau & Resh, 1992) used as a control showed no significant difference among years, indicating that habitat condition remained stable at these sites over time.

Long-term biological monitoring of this restoration project (BC) for 10 years following the initial post-restoration survey indicated that the stream continued to show slow but gradual increases in terms of number of individuals and Shannon's diversity index, and improvements as measured by Family Biotic Index (FBI) and percent numerically dominant taxa (Table 3). In contrast, the unrestored section of Baxter Creek did not show consistent increases in these metrics. However, and perhaps more importantly, the

Table 3 Biological metrics calculated for Baxter Creek (BC in Fig. 1) at Poinsett Park from 1999–2009

Biological metrics	1999	2004	2005	2006	2009
Total no. individuals	2137	1414	1992	2056	4274
Taxa richness	20	15	21	18	18
Percent EPT	1%	0%	1%	19%	1%
Family Biotic Index (FBI)	6.93	6.79	6.50	5.85	6.00
% Coleoptera + Odonata	18%	29%	50%	1%	4%
% Chironomidae	41%	14%	18%	15%	37%
% Numerically dominant taxa	41%	34%	50%	23%	11%
Shannon diversity	1.85	1.50	1.32	1.87	1.90
Evenness	0.66	0.65	0.51	0.68	0.65

EPT refers to the insect orders Ephemeroptera, Plecoptera, and Trichoptera. Sampling methods for each year are those described in Purcell et al. (2002)

restored reach of BC has not attained the richness seen in the control stream, even after a decade.

There are several potential explanations why the restored site on BC did not show dramatic improvements over the course of the long-term study or why it failed to attain a biological condition similar to the control stream. Although all biological samples were collected at the same time of year, using the same sampling methods, and by the same collector, interannual flow variability typical of med-climate streams could have influenced the composition and abundance of biota collected. In addition, the cumulative impacts of urbanization may limit the potential development of the biotic community at the restoration site (e.g., May & Horner, 2000), such as the presence of pollution and increased run-off from the impervious areas (e.g., Walsh & Breen, 1999). Moreover, colonization of additional species could be limited by the short length of the restoration site (70 m) and the presence of culverts at either end that continue for relatively long distances. Both of these factors could result in creating a large distance from sources of potential colonizers.

The steady improvements in habitat conditions observed over a 10-year sampling period at BC is encouraging in the context of restoration goals. However, even longer term study may be needed to show potential development of the biological community.

Protection of stream flow during the wet and dry season favors native species

Components of the natural flow regime related to both the timing and magnitude of flows are critical components of successful habitat management of med-climate streams. For example, the study of Marchetti and Moyle (2001) on PC demonstrated the influence of short-term climatic trends on fish communities, and also highlighted the potential for restoring native fish communities in med-climate systems through restoration of the timing of high and low flow events that are characteristic of these systems. In response to the efforts of a local watershed advocacy group and the results of the Marchetti and Moyle (2001) study, a new flow regime was prescribed based on the outcome of legal action. This new flow regime was "natural" in timing but not magnitude, and was implemented in 2000. Using data collected from 1991 to 2008, including 8 years before and 9 years after the new flow regime was implemented, Kiernan et al. (2012) examined how protection of both high flows during the spring and maintaining lotic conditions throughout the summer influenced the fish community of lower PC. Restoration of the timing of natural flows to this system allowed the native fishes to shift their distribution further downstream and to regain numerical dominance of over 20 km of the 30 km study site. This new flow regime required only a small amount of the available water but the timing of the release of this water captured the seasonality of med-climate streams to which the native fishes are adapted.

Grantham et al. (2012) highlights the importance of protecting the magnitude of summer flows in med-climate California for conservation of a native fish. They examined the effects of summer flows on the survival of threatened steelhead trout (*Oncorhynchus mykiss*) across 9 years of study and found that the summer drought season is a stressful period for these fishes, with survival averaging only 29%. They found that over-summer survival was positively related to summer flow, a result that was highly consistent across the eight stream reaches in the four watersheds that they examined. Like many other coastal California watersheds, their study area near the Russian River (RR) is a region characterized by rapid vineyard expansion and population growth in recent years, which has led to conflicts between human and ecological needs for water (e.g., Deitch et al., 2009; Lawrence et al., 2011).

We expect that such water wars (sensu Poff et al., 2003) between human users of water and native stream fishes will be exacerbated under future climate change. Studies that monitor long-term trends in fish dynamics and that correlate those dynamics to components of the natural flow regime (e.g., the magnitude, frequency, duration, timing, and rate of change of flows; Poff et al., 1997) hold the most promise for protecting stream flow to conserve the inland fishes of California and other med-climate regions. These efforts will likely protect macroinvertebrates in these streams as well.

Conclusion

The studies conducted in Northern California med-climate streams clearly demonstrate the value of long-term data. Moreover, they demonstrate that research or monitoring studies conducted over a single year, or even spanning only a few years, likely will fail to capture the effects of natural variability of freshwater populations and communities. In essence, we believe that interannual variation should be considered as an ongoing, uncontrolled variable that can influence interpretation and conclusions of studies. We believe that recognition of the potential presence of this uncontrolled variable is critical in terms of the ecological understanding of stream dynamics and the development of management considerations. Moreover, it is particularly relevant to med-climate regions throughout the world because of the high variability in the timing and amount of annual precipitation, and consequently stream flow (Gasith & Resh, 1999). In addition, the examples described in this article emphasize that single year and short-term studies can miss infrequent events or longer term cycles in climate, a conclusion also reached by others (e.g., Eby et al., 2003; Lake, 2003; Jackson & Füreder, 2006; Dodds et al., 2012). Likewise, climatic changes and the associated increases in hydro-climatic extremes that are anticipated, such as prolonged and intensified drought in med-regions, can result in dramatic changes or gradual shifts in freshwater populations and communities and their processes (e.g., Bady et al., 2004; Bêche & Resh, 2007a, b; Chase, 2007; Daufresne et al., 2004; Durance & Ormerod, 2007, 2009).

Long-term data is required to accurately differentiate the effects of natural variability (e.g., from natural floods or droughts) from human impacts (Gasith & Resh, 1999; Bêche et al., 2009). This will require adjustments to existing monitoring protocols and analyses. Moreover, in med-climate regions the increasing demand for water (e.g., Gasith & Resh, 1999; Barnett et al., 2008; Grantham et al., 2010), coupled with natural drought cycles and climate change, will likely have increasingly dramatic effects on streams and related ecosystems, including riparian areas, hyporheic zones, freshwater wetlands (e.g., vernal pools, ponds, and lakes), and even estuaries fed by coastal streams. Long-term data may enable us to better manage these sensitive ecosystems for multiple users (e.g., municipal, industrial, agricultural, and recreational) by providing an appropriate framework for developing thresholds for environmental flows across seasons and years by incorporating the magnitude, variability, and water quality needed to support these systems (e.g., Grantham et al., 2010).

The huge financial investment made in biological assessment surveys in the United States (Carter & Resh, 2001) and other developed countries (Bonada et al., 2006) assumes that natural and anthropogenic variability can be distinguished across both space and time, although few, applicable long-term datasets have been used to test whether this assumption is correct in different climate regions (e.g., Bradley & Omerod, 2001; Metzeling et al., 2002). The high temporal variability in med-climate regions underscores the need to better understand appropriate reference conditions, such as using appropriate reference periods, for temporal comparisons. Perhaps studies that have quantified the value of the ecosystem services fresh waters provide (e.g., the benefits that people obtain from these ecosystems) may increase public support for investment in long-term data collection (Brauman et al., 2007).

We believe that the case studies described from Northern California streams demonstrate clearly how the availability of long-term data can provide the basis for invaluable retrospective analyses of both populations and communities of benthic macroinvertebrates and fishes in med-climate regions. Analyses based on long-term data may enable quantitative, transparent, and defensible predictions that can inform both water resources management, including biological-monitoring programs and ecological restoration projects, as well as advance future experimental and theoretical studies in ecology. The usefulness of such long-term datasets for the latter is illustrated by the knowledge gained from a study of freshwater food webs using 18 years of field observations of benthic macroinvertebrates, fishes, algae, and cyanobacteria collected from a med-climate California river (Power et al., 2008, 2012).

The relatively few long-term, consistently collected datasets available for streams in most of the highly seasonal rainfall regions of the world (e.g., monsoonal areas) is clearly a hindrance to both the application of management strategies and a better understanding of the ecology of these systems (Lévêque et al., 2003). This lack of information can only be remedied by making funding for long-term studies a priority. Med-climate regions of the world, which are important centers of human populations and sustenance, and are especially vulnerable to human influences on local and global scales, may be the most appropriate place to start this process.

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References

Bady, P., S. Dolédec, B. Dumont & J. Fruget, 2004. Multiple co-inertia analysis: a tool for assessing synchrony in the temporal variability of aquatic communities. Comptes Rendus Biologies 327: 29–36.

Bailey, R. C., R. H. Norris & T. B. Reynoldson, 2003. Bioassessment of freshwater ecosystems: using the reference condition approach. Kluwer Academic Publishers, Boston.

Ball, J. E., L. A. Bêche, P. K. Mendez & V. H. Resh, 2012. Biodiversity in mediterranean-climate streams of California. Hydrobiologia. doi:10.1007/s10750-012-1368-6.

Barbour, M. T., J. Gerritsen, B. D. Snyder & J. B. Stribling, 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, 2nd edition. EPA 841-B-99-002. US Environmental Protection Agency, Office of Water, Washington, DC.

Barnett, T. P., D. W. Pierce, H. G. Hidalgo, C. Bonfils, B. D. Santer, T. D. G. Bala, A. W. Wood, T. Nozawa, A. A. Mirin, D. R. Cayan & M. D. Dettinger, 2008. Human-induced changes in the hydrology of the western United States. Science 319: 1080–1083.

Bêche, L. A. & V. H. Resh, 2007a. Biological traits of benthic macroinvertebrates in California Mediterranean-climate streams: long-term annual variability and trait diversity patterns. Fundamental and Applied Limnology 169: 1–23.

Bêche, L. A. & V. H. Resh, 2007b. Short-term climatic trends affect the temporal variability of macroinvertebrates in California 'mediterranean' streams. Freshwater Biology 52: 2317–2339.

Bêche, L. A., E. P. McElravy & V. H. Resh, 2006. Long-term seasonal variation of benthic-macroinvertebrate biological traits in two mediterranean-climate streams in California, USA. Freshwater Biology 51: 56–75.

Bêche, L. A., P. G. Connors, V. H. Resh & A. M. Merenlender, 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. Ecography 32: 778–788.

Bernardo, J. M., M. Ilhéu, P. Matono & A. M. Costa, 2003. Interannual variation of fish assemblage structure in a Mediterranean River: implications of streamflow on the dominance of native or exotic species. River Research and Applications 19: 521–532.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell & E. Sudduth, 2005. Synthesizing US river restoration efforts. Science 308: 636–637.

Blumenshine, S. C., B. Tsukimura, A. Rice & D. A. Rudnick, 2012. Environmental factors influencing the dynamics of Chinese mitten crabs in the San Francisco Bay-Delta. Aquatic Invasions 7: 111–124.

Bogan, M. T. & D. A. Lytle, 2011. Severe drought drives novel community trajectories in desert stream pools. Freshwater Biology 56: 2070–2081.

Bonada, N., 2003. Ecology of the macroinvertebrate communities in mdeiterranean rivers at different scales and organization levels. Ph.D. thesis. University of Barcelona, Spain.

Bonada, N., M. Rieradevall, N. Prat & V. H. Resh, 2006. Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean climate streams of northern California. Journal of the North American Benthological Society 25: 32–43.

Bonada, N., M. Rieradevall & N. Prat, 2007. Interaction of spatial and temporal heterogeneity: constraints on macroinvertebrate community structure and species traits in a Mediterranean river network. Hydrobiologia 589: 91–106.

Bond, N. R., P. S. Lake & A. H. Arthington, 2008. The impacts of drought on freshwater ecosystems: an Australian perspective. Hydrobiologia 600: 3–16.

Boulton, A. J., C. G. Peterson, N. B. Grimm & S. G. Fisher, 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrological disturbance regime. Ecology 73: 2102–2207.

Bradley, D. C. & J. Ormerod, 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. Journal of Animal Ecology 70: 987–996.

Brauman, K. A., G. C. Daily, T. K. Duarte & H. A. Mooney, 2007. The nature and value of ecosystem services: an overview highlighting hydrologic services. Annual Review of Environment and Resources 32: 67–98.

Briers, R. A., J. H. R. Gee & R. Geoghegan, 2004. Effects of the North Atlantic Oscillation on growth and phenology of stream insects. Ecography 27: 811–817.

Brook, B. W. & C. J. A. Bradshaw, 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87: 1445–1451.

Burt, T. P., N. J. K. Howden, F. Worrall & M. J. Whelan, 2008. Importance of long-term monitoring for detecting environmental change: lessons from a lowland river in south east England. Biogeosciences Discussions 5: 2369–2379.

Carlisle, D. M. & W. H. Clements, 1999. Sensitivity and variability of metrics used in biological assessments of running waters. Environmental toxicology and chemistry 18: 285–291.

Carter, J. L. & V. H. Resh, 2001. After site selection and before data analysis: sampling sorting, and laboratory procedures used in stream benthic-macroinvertebrate monitoring programs by USA state agencies. Journal of the North American Benthological Society 20: 658–682.

Cattanéo, F., N. Lamouroux, P. Breil & H. Capra, 2002. The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 59: 12–22.

Charbonneau, R. & V. H. Resh, 1992. Strawberry Creek on the University of California, Berkeley campus: a case history of urban stream restoration. Aquatic Conservation 2: 293–307.

Chase, J. M., 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences USA 104: 17430–17434.

Chessman, B. C., 2009. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. Global Change Biology 15: 2791–2802.

Chessman, B. C., H. A. Jones, N. K. Searle, I. O. Growns & M. P. Parsons, 2010. Assessing effects of flow alteration on macroinvertebrate assemblages in Australian dryland rivers. Freshwater Biology 55: 1780–1800.

Chester, E. T. & B. J. Robson, 2011. Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. Freshwater Biology 56: 2094–2104.

Chin, A., A. H. Purcell, J. Quan & V. H. Resh, 2009. Assessing geomorphological and ecological responses in restored step-pool systems. In James, L. A., S. L. Rathburn & G. R. Whittcar (eds), Management and Restoration of Fluvial Systems with Broad Historical Changes and Human Impacts. Geological Society of America Special Paper 451, Boulder, CO: 199–217.

Connell, J. H. & W. P. Sousa, 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121: 789–824.

Cooper, S. D., T. L. Dudley & N. Hemphill, 1986. The biology of chaparral streams in Southern California. In DeVries, J. (ed.), Proceedings of the Chaparrel Ecosystem Research Conference Report no. 62. California Water Resources Center, Davis, CA: 139–151.

Daufresne, M., M. C. Roger, H. Capra & N. Lamarouroux, 2004. Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. Global Change Biology 10: 124–140.

Daufresne, M., P. Bady & J.-F. Fruget, 2007. Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhône River. Oecologia 151: 544–559.

Daufresne, M., K. Lengfellner & U. Sommer, 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences 106: 12788–12793.

Deitch, M. J., G. M. Kondolf & A. M. Merenlender, 2009. Hydrologic impacts of small-scale instream diversions for frost and heat protection in the California wine country. River Research and Applications 25: 118–134.

Dewson, Z. S., A. B. W. James & R. G. Death, 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. Journal of the North American Benthological Society 26: 401–415.

Didham, R. K. & C. H. Watts, 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? Oikos 110: 409–416.

Dodds, W. K., C. T. Robinson, E. E. Gaiser, G. J. A. Hansen, H. Powell, J. M. Smit, N. B. Morse, S. L. Johnson, S. V. Gregory, T. K. Kratz & W. H. McDowell, 2012. Surprises and insights from long-term data sets and experiments. BioScience 62: 709–721.

Doeg, T. J., 1996. An assessment of significance of the aquatic macroinvertebrates in the Grampians National Park. National Estate Grants Program No. 95/0025. Final Report, Department of Natural Resources and Environment, Victoria and Australian Heritage Commission, Canberra.

Durance, I. & S. J. Ormerod, 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. Global Change Biology 13: 924–957.

Durance, I. & S. J. Ormerod, 2009. Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. Freshwater Biology 54: 388–405.

Eby, L. A., W. F. Fagan & W. L. Minckley, 2003. Variability and dynamics of a desert stream community. Ecology 13: 1566–1579.

Elliott, J. M., 1990. The need for long-term investigations in ecology and the contribution of the Freshwater Biological Association. Freshwater Biology 23: 1–5.

Elliott, J. M., 1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta,* in an English Lake District stream. Canadian Special Publication of Fisheries and Aquatic Sciences 118: 109–122.

Elliott, J. M., 1994. Quantitative ecology and the brown trout. Oxford University Press, New York.

Feminella, J. W. & V. H. Resh, 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. Ecology 71: 2083–2094.

Filipe, A. F., J. E. Lawrence & N. Bonada, 2012. Vulnerability of stream biota to climate change in mediterranean climate regions: a synthesis of ecological responses and conservation challenges. Hydrobiologia. doi:10.1007/s10750-012-1244-4.

Franken, R. J. M., R. G. Storey & D. D. Williams, 2001. Biological, chemical and physical characteristics of downwelling and upwelling zones in the hyporheic zone of a north-temperate stream. Hydrobiologia 444: 183–195.

Gallo, L., A. De Filippis, A. Mezzotero, N. J. Voelz & L. Lucadamo, 2010. Assessment of the effect of hydrological variations on macrobenthic communities in pools and riffles of a Mediterranean stream. Environmental Monitoring and Assessment 166: 125–137.

Gasith, A. & V. H. Resh, 1999. Streams in mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annual Review of Ecology and Systematics 31: 51–81.

Gebler, J. B., 2004. Mesoscale spatial variability of selected aquatic invertebrate community metrics from a minimally impaired stream segment. Journal of the North American Benthological Society 23: 616–633.

Grantham, T. E., A. M. Merenlender & V. H. Resh, 2010. Climatic influences and anthropogenic stressors: an integrated framework for streamflow management in Mediterranean-climate California, USA. Freshwater Biology 55(Suppl. 1): 188–204.

Grantham, T. E., D. A. Newburn, M. A. McCarthy & A. M. Merenlender, 2012. The role of stream flow and land use in limiting over-summer survival of juvenile steelhead trout in California streams. Transactions of the American Fisheries Society 141: 585–598.

Haddad, N. M., D. Tilman & J. M. H. Knops, 2002. Long-term oscillations in grassland productivity induced by drought. Ecological Letters 5: 110–120.

Hannaford, M. J. & V. H. Resh, 1995. Variability in macroinvertebrate rapid-bioassessment surveys and habitat assessments in a Northern California stream. Journal of the North American Benthological Society 14: 430–439.

Hannaford, M. J., M. J. Barbour & V. H. Resh, 1997. Training reduces observer variability in visual-based assessments of stream habitat. Journal of the North American Benthological Society 16: 853–860.

Hieb, K., 2009. 2008 status and trends report: common crabs of the San Francisco Estuary. IEP Newsletter 22: 12–16.

Hieb, K., 2010. 2009 status and trends report: common crabs of the San Francisco Estuary. IEP Newsletter 23: 22–28.

IPCC, 2008. Climate Change and Water. In Bates, B. C., Z. W. Kundzewicz, S. Wu & J. P. Palutikof (eds), Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva: 1–200.

Jackson, J. K. & L. Füreder, 2006. Long-term studies of freshwater macroinvertebrates: a review of frequency, duration and ecological significance. Freshwater Biology 51: 591–603.

Kiernan, J. D., P. B. Moyle & P. K. Crain, 2012. Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. Ecological Applications 22: 1472–1482.

Kondolf, G. M., 1995. Five elements for effective evaluation of stream restoration. Restoration Ecology 3: 133–136.

Kondolf, G. M., 1998. Lessons learned from river restoration projects in California. Aquatic Conservation: Marine and Freshwater Ecosystems 8: 39–52.

Kondolf, G. M. & E. R. Mitchell, 1995. Evaluating stream restoration projects. Environmental Management 19: 1–15.

Kondolf, G. M., K. Podolak & T. E. Grantham, 2012. Restoring mediterranean-climate rivers. Hydrobiologia. doi:10.1007/s10750-012-1363-y.

Labbe, T. R. & K. D. Fausch, 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10: 1774–1791.

Lake, P. S., 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19: 573–592.

Lake, P. S., 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48: 1161–1172.

Lake, P. S., 2008. Drought, the "creeping disaster". Effects on Aquatic Ecosystems. Land & Water Australia, Canberra.

Lamberti, G. A. & V. H. Resh, 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64: 1124–1135.

Lawrence, J. E., K. E. Lunde, R. D. Mazor, L. A. Bêche, E. P. McElravy & V. H. Resh, 2010. Long-term macroinvertebrate response to climate change: implications for biological assessment in mediterranean-climate streams. Journal of the North American Benthological Society 29: 1424–1440.

Lawrence, J. E., M. J. Deitch & V. H. Resh, 2011. Effects of Vineyard Coverage and Extent on Benthic Macroinvertebrates in Mediterranean-Climate Streams of Northern California. Annales de Limnologie - International Journal of Limnology 47: 347–354.

Lenat, D. R. & V. H. Resh, 2001. Taxonomy and stream ecology—the benefits of genus- and species-level identifications. Journal of the North American Benthological Society 20: 287–298.

Lévêque, C., J. M. Hougard, V. H. Resh, B. Statzner & L. Yaméogo, 2003. Freshwater ecology and biodiversity in the tropics: what did we learn from 30 years of Onchocerciasis control and the associated biomonitoring of West African rivers? Hydrobiologia 500: 23–49.

Linke, S., R. C. Bailey & J. Schwindt, 1999. Temporal variability of stream bioassessments using benthic macroinvertebrates. Freshwater Biology 42: 575–584.

Lunde, K.B., 2011. Investigations of altered aquatic ecosystems: biomonitoring, disease, and conservation. Ph.D. thesis, University of California, Berkeley, CA.

Magalhães, M. F., P. Beja, I. J. Schlosser & M. G. Collares-Pereira, 2003. The role of life history in the relationship between population dynamics and environmental variability in two Mediterranean stream fishes. Journal of Fish Biology 63: 300–317.

Magalhães, M. F., P. Beja, I. J. Schlosser & M. G. Collares-Pereira, 2007. Effects of multi-year droughts on fish assemblages of seasonally drying Mediterranean streams. Freshwater Biology 52: 1494–1510.

Magurran, A. E., 2007. Species abundance distributions over time. Ecology Letters 10: 347–354.

Marchetti, M. P. & P. B. Moyle, 2000. Spatial and temporal ecology of native and introduced fish larvae in lower Putah Creek, California. Environmental Biology of Fishes 58: 75–87.

Marchetti, M. P. & P. B. Moyle, 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11: 530–539.

Matthews, W. J. & E. Marsh-Matthews, 2003. Effects of drought on fish across axes of space, time and ecological complexity. Freshwater Biology 48: 1232–1253.

May, C. W. & R. R. Horner, 2000. The cumulative impacts of watershed urbanization on stream-riparian ecosystems. In Wigington, P. J. & R. L. Beschta (eds), Proceedings of the International Conference on Riparian Ecology and Management in Multi-Land Use Watersheds. American Water Resources Association, Portland: 281–286.

Mazor, R. D., 2006. Evaluation of biomonitoring techniques using benthic macroinvertebrates and periphyton in aquatic ecosystems: detecting impairment of population and community structure. Ph.D. thesis, University of California, Berkeley, CA.

Mazor, R., A. Purcell & V. H. Resh, 2009. Long-term variability in benthic macroinvertebrate bioassessments: a 20-year study from two northern Californian streams. Environmental Management 43: 1269–1286.

McElravy, E. P. & V. H. Resh, 1991. Distribution and seasonal occurrence of the hyporheic fauna in a northern California stream. Hydrobiologia 220: 233–246.

McElravy, E. P., G. A. Lamberti & V. H. Resh, 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. Journal of the North American Benthological Society 8: 51–63.

Metzeling, L. D., S. Perriss Robinson & R. Marchant, 2002. Temporal persistence of benthic invertebrate communities in south-eastern Australian streams: taxonomic resolution and implications for the use of predictive models. Marine and Freshwater Research 53: 1223–1234.

Milner, A. M., S. C. Conn & I. E. Brown, 2006. Persistence and stability of macroinvertebrate communities in streams of Denali National Park, Alaska: implications for biomonitoring. Freshwater Biology 51: 357–373.

Mol, J. H., D. Resida, J. S. Ramlal & C. R. Becker, 2000. Effects of El Niño-related drought on freshwater and brackishwater fishes in Suriname, South America. Environmental Biology of Fishes 59: 429–440.

Morais, M., P. Pinto, P. Guilherme, J. Rosado & I. Antunes, 2004. Assessment of temporary streams: the robustness of metric and multimetric indices under different hydrological conditions. Hydrobiologia 516: 229–249.

Moyle, P. B., 2002. Inland fishes of California. University of California Press, Berkeley.

Moyle, P. B., P. K. Crain, K. Whitener & J. F. Mount, 2003. Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, USA. Environmental Biology of Fishes 68: 143–162.

Needham, P. R. & R. L. Usinger, 1956. Variability in the macrofauna of a single riffle in Prosser Creek, California, as indicated by the Surber sampler. Hilgardia 24: 383–409.

Oberdorff, T., B. Hugueny & T. Vigneron, 2001. Is assemblage variability related to environmental variability? An answer for riverine fishes. Oikos 93: 419–428.

Ode, P. R., A. C. Rehn & J. T. May, 2005. A quantitative tool for assessing the integrity of southern coastal California streams. Environmental Management 35: 493–504.

Ode, P. R., C. P. Hawkins & R. D. Mazor, 2008. Comparability of biological assessments derived from predictive models and multimetric indices of increasing geographic scope. Journal of the North American Benthological Society 27: 967–985.

Pillot, H. M., 2003. Hoe waterdieren zich handhaven in een dynmische wereld. 10 jaar onderzoek in de Roodloop, een bovenloopje van der Reusel in Noord-Brabant. Stichting het Noordbrabants Landschap, Haaren, The Netherlands.

Pires, A. M., I. G. Cowx & M. M. Coelho, 1999. Seasonal changes in fish community structure of intermittent streams in the middle reaches of the Guadiana basin, Portugal. Journal of Fish Biology 54: 235–249.

Pires, A. M., I. G. Cowx & M. M. Coelho, 2000. Benthic macroinvertebrate communities of intermittent streams in the middle reaches of the Guadiana Basin (Portugal). Hydrobiologia 435: 167–175.

Poff, N. L. & J. D. Allan, 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. Ecology 76: 606–627.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks & J. C. Stromberg, 1997. The natural flow regime. Bioscience 47: 769–784.

Poff, N. L., J. D. Allen, M. A. Palmer, D. D. Hard, B. D. Richter, A. H. Arthington, K. H. Rogers, J. L. Meyer & J. A. Stanford, 2003. River flows and water waters: emerging science for environmental decision making. Frontiers in Ecology and the Environment 1: 298–306.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner & I. R. Wais de Badgen, 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7: 456–479.

Power, M. E., M. S. Parker & W. E. Dietrich, 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. Ecological Monographs 78: 263–282.

Power, M. E., J. Holomuzki & R. L. Lowe, 2012. Food webs in mediterranean rivers. Hydrobiologia, this issue.

Puckridge, J. T., K. F. Walker & J. F. Costelloe, 2000. Hydrological persistence and the ecology of dryland rivers. Regulated Rivers: Research and Management 16: 328–344.

Purcell, A. H., C. Friedrich & V. H. Resh, 2002. An assessment of a small urban stream restoration project in northern California. Restoration Ecology 10: 685–694.

Rehn, A. C., P. R. Ode & J. T. May, 2005. Development of a benthic index of biotic integrity (B-IBI) for wadable streams in in northern coastal California and its application to regional 305(b) assessment. Report to the State Water Resources Control Board. California Department of Fish and Game, Aquatic Bioassessment Laboratory.

Rieradevall, M., N. Bonada & N. Prat, 1999. Community structure and water quality in the mediterranean streams of a natural park (St. Llorenç del Munt, EN Spain). Limnetica 17: 45–56.

Resh, V. H., 1982. Age structure alteration in a caddisfly population following loss and recovery of habitat. Oikos 38: 280–284.

Resh, V. H., 1992. Year-to-year changes in the age structure of a caddisfly population following loss and recovery of a springbrook habitat. Ecography 15: 314–317.

Resh, V. H., 1994. Variability, accuracy, and taxonomic costs of rapid assessment approaches in benthic biomonitoring. Bolletino di Zoologia 61: 375–383.

Resh, V. H. & J. K. Jackson, 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In Rosenberg, D. M. & V. H. Resh (eds), Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York: 195–223.

Resh, V. H. & D. M. Rosenberg, 1989. Spatial-temporal variability and the study of aquatic insects. Canadian Entomologist 121: 941–963.

Resh, V. H. & D. M. Rosenberg, 2010. Recent trends in life-history research on benthic macroinvertebrates. Journal of the North American Benthological Society 29: 207–219.

Resh, V. H., G. A. Lamberti & J. R. Wood, 1984. Biology of the caddisfly *Helicopsyche borealis* (Hagen): A comparison of North American populations. Freshwater Invertebrate Biology 5: 172–180.

Resh, V. H., A. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, W. Minshall, S. Reice, A. L. Sheldon, J. B. Wallace & R. Wissmar, 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7: 433–455.

Resh, V. H., R. H. Norris & M. T. Barbour, 1995. Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. Australian Journal of Ecology 20: 108–121.

Resh, V. H., J. R. Wood, E. A. Bergey, J. W. Feminella, J. K. Jackson & E. P. McElravy, 1997. Biology of *Gumaga nigricula* (McL.) in a northern California stream. In Holzenthal, R. & O. Flint (eds), Proceedings of the 8th International Symposia on Trichoptera. Ohio Biological Survey, Columbus, OH: 401–410

Resh, V. H., L. Bêche & E. P. McElravy, 2005. How common are rare species in long-term benthic macroinvertebrate studies? Journal of the North American Benthological Society 24: 976–989.

Reynoldson, T. B., R. H. Norris, V. H. Resh, K. E. Day & D. M. Rosenberg, 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water quality impairment using benthic macroinvertebrates. Journal of the North American Benthological Society 16: 833–852.

Rose, P., L. Metzeling & S. Catzikiris, 2008. Can macroinvertebrate rapid bioassessment methods be used to assess river health during drought in south eastern Australia streams? Freshwater Biology 53: 2626–2638.

Rosenberg, D. M. & V. H. Resh, 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Rudnick, D. & V. H. Resh, 2005. Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod crustacea. Freshwater Biology 50: 1323–1336.

Rudnick, D., K. Halat & V. H. Resh, 2000. Distribution, ecology and economic impacts of the Chinese Mitten Crab (*Eriocheir sinensis*) in San Francisco Bay. University of California Water Resources Center Contribution 206, Davis, CA.

Rudnick, D., K. Hieb, K. Grimmer & V. H. Resh, 2003. Patterns and processes of biological invasion: the Chinese mitten crab in San Francisco Bay. Basic and Applied Ecology 4: 249–262.

Rudnick, D., V. Chan & V. H. Resh, 2005. Morphology and impacts of the burrows of the Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards (Decapoda, Grapsidae) in South San Francisco Bay, California, USA. Crustaceana 78: 787–807.

Scarsbrook, M. R., I. K. G. Boothroyd & J. M. Quinn, 2000. New Zealand's national river water quality network: long-term trends in macroinvertebrate communities. New Zealand Journal of Marine and Freshwater Research 34: 289–302.

Scheffer, M., D. Straile, E. H. van Nes & H. Hosper, 2001. Climate warming causes regime shifts in lake food webs. Limnology and Oceanography 46: 1780–1783.

Storey, R. G. & D. D. Williams, 2004. Spatial responses of hyporheic invertebrates to seasonal changes in environmental parameters. Freshwater Biology 49: 1468–1486.

Townsend, C., S. Dolédec & M. Scarsbrook, 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. Freshwater Biology 37: 367–387.

Wagner, R., J. Marxsen, P. Zwick & E. J. Cox, 2009. Central European stream ecosystems The long term study of the Breitenbach. Wiley-Blackwell, Weinheim.

Walsh, C. J. & P. F. Breen, 1999. Urban stream rehabilitation through a decision-making framework to identify degrading processes and prioritize management actions. In Rutherfurd, I. & R. Bartley (eds), Proceedings of the Second Australian Stream Management Conference, Adelaide S.A. Vol 2. Cooperative Research Centre for Catchment Hydrology, Melbourne: 763–768.

Walters, A. W. & D. M. Post, 2008. An experimental disturbance alters fish size structure but not food chain length in streams. Ecology 89: 3261–3267.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg & F. Bairlein, 2002. Ecological responses to recent climate change. Nature 416: 389–395.