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

Vincent H. Resh[1], Leah A. Bêche[1], Justin E. Lawrence[1], Raphael D. Mazor[2], Eric P. McElravy[1], Alison P. O'Dowd[3], Deborah Rudnick[1] and Stephanie M. Carlson[1]*

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 management practices and development of appropriate ecological constructs.

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 and Rosenberg 2010). With the onset of formalized ecological studies, however, most research described results from single observations or from patterns evident from

[1]*University of California, Department of Environmental Science, Policy and Management, Berkeley, CA*

[2]*California Department of Fish and Game, Rancho Cordova, CA*

[3]*Humboldt State University, Department of Environmental Science and Management, Arcata, CA*

*Present Address: Integral Consulting, Inc., Seattle, WA

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 and Rosenberg 1989; Rosenberg and Resh 1993; Elliott 1993, 1994; Jackson and Füreder 2006). However, because 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 and Sousa 1983, Elliott 1990, Brook and Bradshaw 2006, Jackson and 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, 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 and 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 and Omerod 2001; Briers *et al.* 2004; Durance and Omerod 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 and 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 and Ormerod 2007, 2009).

Seasonal and annual variability in community structure is often high in streams (Poff and Allan 1995, Townsend *et al.* 1997, Daufresne *et al.* 2004) and is 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 and 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 and 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, 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 and 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 (Figure 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 (Figure 2). Sites include: streams originating from spring seepages (Hopland Springs [HOP], 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], 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 and Usinger 1956) and taxonomic errors (Lenat and 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-yr studies conducted at some of the areas examined (HOP, KC, HC, PC) are the most consistent long-term data-sets for benthic macroinvertebrates available worldwide in that all
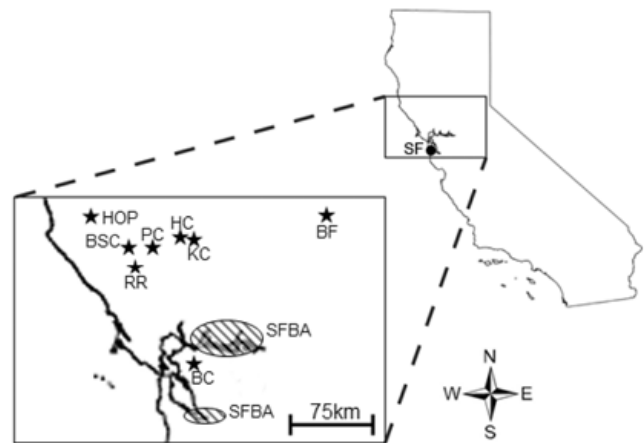

Figure 1. Map of study sites in the med-climate region of California (see Ball et al. 2012 issue for description of the med-climate region in this state). Stars indicate study sites: Hopland Springs (HOP), Hunting Creek (HC), Knoxville Creek (KC), Big Sulfur Creek (BSC), Blodgett Forest (BF), Baxter 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).

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,

Table 1. Description of study sites in the med-climate region of California. Stream location is found in Figure 1.

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 and Resh 1983; Bêche *et al.* 2006; McElravy *et al.* 1989
Blodgett Forest (BF)	5	8 years (1995-2004)	1-2	Bêche and Resh 2007
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 and Moyle 1995; Kiernen *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
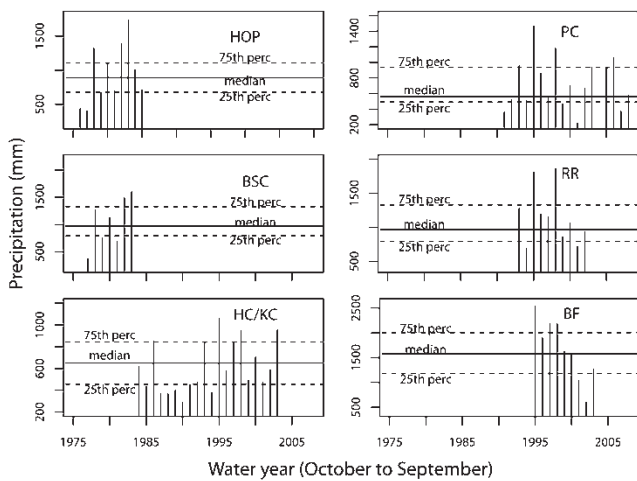
Figure 2. Annual precipitation for each water year (October of the previous calendar year to September of the following year) during the time period that studies were conducted at the different sites listed in Table 1. The median, 25th and 75th percentile values are based on long-term time series for 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).

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 from non-mediterranean areas do exist (e.g., 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 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 to the drought that started in 1976 was dominated by early instars with pupae present year-round, reflect-ing a multi-cohort population. Surveys following resumption of flow indicated that no *G. nigricula* larvae survived this drought. In 1979, two years after habitat recovery, surveys indicated that although this species had recolonized, the age structure had changed. A single cohort population was now present, and a clear succession in the numerical dominance of age classes proceeding from early to late instars was evident over time (Figure 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 multi-cohort to a single-cohort population occurred within one 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 (Figure 3).

This long recovery period could have been the result of drought-induced population-density decrease or the lack of food availability. For ex-ample, 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
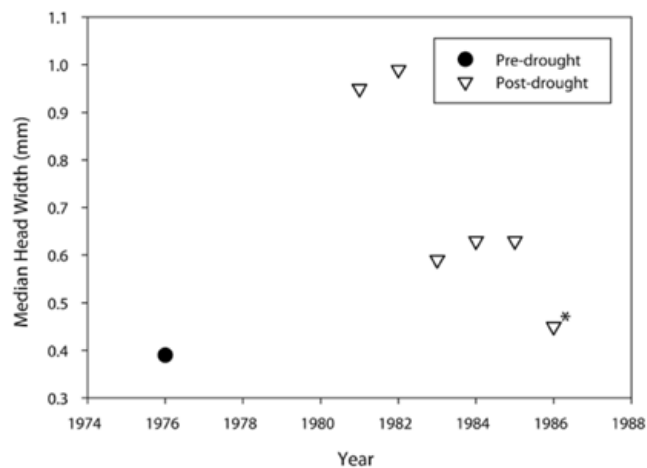
Figure 3. Temporal changes in head capsule width for Gumaga nigricula before (1976) and after (1981-1986 the loss of its habitat as a result of extreme drought (data from Resh 1982, 1992). * indicates χ² not significantly different from 1976 pre-drought value; t-test, p-value of <0.001.

gradually increasing to >1,000/m². 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, 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 and 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 towards 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) (Figure 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 two to five 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 (Figure 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,
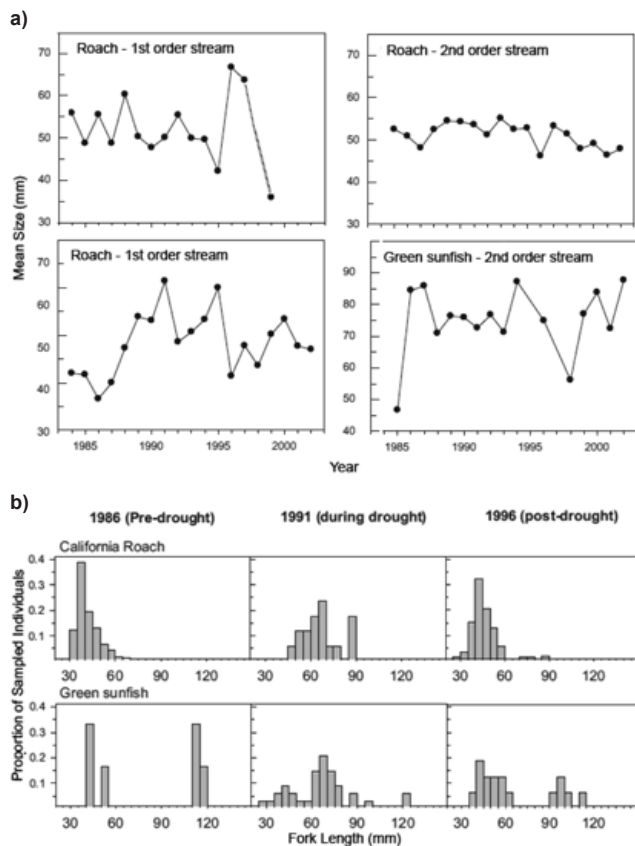
Figure 4. Annual changes in mean size for California roach at three sites, and green sunfish at one site (a). Size distribution of both species in three years found at one second-order stream, demonstrating pre-drought (1986), drought (1991), and post-drought (1996) population patterns (b; data from Bêche et al. 2009).

Figure 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.

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) (Figure 4).

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 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 and 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 (e.g., Gasith and 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 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 and 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 and 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 and 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 (Figure 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 macro-invertebrate 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 and 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 lowest during the drought years and highest during the following wet years (see also Marchetti and 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 (Figure 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 and Resh 2007a,b).

Alternative stable states are expected to be more common in systems with strong underlying abiotic regimes (Didham and Watts 2005), such as streams (Resh *et al.* 1988), and especially for streams in med-climates (Gasith and Resh 1999). Examples of such alternative stable states in stream ecosystems include restoration efforts that failed to result in "recovery" in community composition (Didham and Watts 2005). In the case of the non-perennial site examined in HC, a press disturbance altered the physical and biologi-cal 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 and 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 becomes 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 and 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-yr 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 highest in the non-perennial stream in the dry season (ranging from a dry stream bed to a flowing stream) but 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 and 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 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, because 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-stream 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 nonnatives to one dominated by natives (Marchetti and 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 nonnative 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 there 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 and Moyle 2001). This combination of traits (i.e., spring spawning, long-lived, high adult survivorship) is also found in to 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 one 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 towards 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 and 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 and Jackson 1993, Resh 1994). Seasonal variability in benthic-macroinvertebrate communities arises from both physical (e.g., reduced flow, lower oxygen concentrations; Gasith and Resh 1999) and biological (e.g., predation and competition; Power *et al.* 1988, Power *et al.* 2008) factors that may alter community composition. 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 and 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 and Resh 1993). 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 and Resh 1999, Morais 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 and 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 to 4 years of collections for index development or model calibration (Mazor *et al.* 2009). We believe that more

Table 2. Seasonal and annual variability for metrics examined. 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).

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
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

Table 2. Continued

Metric	Seasonal Variability			Annual Variability		
	Mean CV	Std. Dev.	Range	Mean CV	Std. Dev.	Range
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 / y	66	29	7-127	90	22	70-120
% 1 gen / y	17	17	0-56	15	6	7-21
% > 1 gen / y	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
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 / y	62	31	13-117	84	18	70-109
% 1 gen / y	16	14	1-50	18	6	12-26
% > 1 gen / y	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

detailed evaluation of the amount of annual variability in various in biological-monitoring metrics is a critical, and much needed, future step towards 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 (Figure 6). In the moving-windows approach (Figure 6a), a fixed nuber of years before the test year were used to etablish the reference period. The reference condition was recalibrated each year as new data were available, and older data were ignored. In the growing-windows approach (Figure 6b), 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 (Figure 6c) 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.
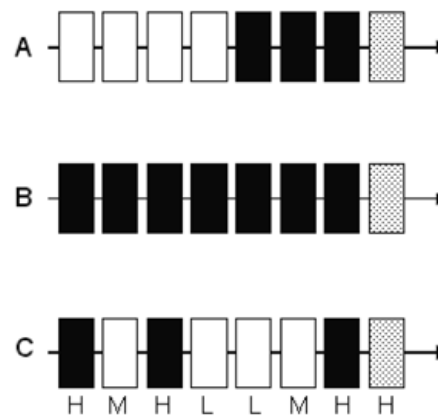
Figure 6. Three approaches to establishing reference periods with long term data: moving window (a), growing window (b), and rainfall based (c). Each rectangle represents a year of biological data, and arrows indicate the passage of time. Black squares represent years used to establish the reference 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 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 (Figure 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 six 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 and Clements 1999). Long-term data are essential to do this in an appropriate manner.

Long-term data can be used to monitor and to 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 data sets (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 and 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 to 20 years of collections and compared these to two shorter, 7-year (BF) and 8-year (BSC), data sets 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 one 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 and 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 data sets currently available that we could find for comparison, Resh *et al.* (2005) did compare their results with a macroinvertebrate data set 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 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 and 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 data sets, 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 nonnative invasive species, as has been demonstrated above for fish communities in HC and PC. Moreover, nonnative 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, 2005a,b). *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 2009-10, no crabs were collected in the numerous, detailed surveys conducted in 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 and 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 and Resh 1992) used as a control showed no significant difference between 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 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 and Horner 2000), such as the presence of pollution and increased run-off from the impervious areas (e.g., Walsh and Breen 1999). Moreover, colonization of additional species could be limited by the short length of the restoration site

Table 3. Biological metrics calculated for Baxter Creek (BC in Figure 1) at Poinsett Park from 1999-2009. EPT refers to the insect orders Ephemeroptera, Plecoptera, and Trichoptera. Sampling methods for each year are those described in Purcell *et al.* (2002).

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	6.5	5.85	6
% 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	1.5	1.32	1.87	1.9
Evenness	0.66	0.65	0.51	0.68	0.65

(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 to2008, including eight years before and nine 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 important 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 nine 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 and 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 and 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, Beche and Resh 2007a, 2007b, Chase 2007, Daufresne *et al.* 2004, Durance and Omerod 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 and 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 and 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, 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, 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 and Resh 2001) and other developed countries (Bonada *et al.* 2006) assume that natural and anthropogenic variability can be distinguished across both space and time, although few, applicable long-term data sets have used to test whether this assumption is correct in different climate regions (e.g., Bradley and 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 data sets 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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