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Long-term macroinvertebrate responses to climate change: implications for biological assessment in mediterranean-climate streams

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Abstract. Climate change is expected to have strong effects on mediterranean-climate regions worldwide. In some areas, these effects will include increases in temperature and decreases in rainfall, which could have important implications for biological assessment programs of aquatic ecosystems. We used a consistently collected, 20-y benthic macroinvertebrate data set from 4 sites along 2 small northern California streams to examine potential climate-change effects on aquatic communities. The sites represented unique combinations of stream order and flow intermittency. The North Coast benthic macroinvertebrate index of biotic integrity (B-IBI) developed for northern California streams was not influenced by temperature extremes (cool and warm) or precipitation extremes (wet and dry). Other common indices and metrics used in biological monitoring studies, such as the ratio of observed to expected taxa (O/E), % Ephemeroptera, Plecoptera, and Trichoptera (EPT) individuals, and total richness were unaffected by temperature and precipitation variability. For future monitoring of climate-change effects on small streams, we developed a local climate-change indicator that is composed of the presence/absence of 9 macroinvertebrate taxa, identified to genus level. This indicator detected significant differences between years that were grouped based on temperature, precipitation, and a combination of temperature and precipitation. It also detected significant differences between groups in an external data set including 40 reference sites throughout the San Francisco Bay area, a result that suggests this indicator could be used at larger spatial scales in this region. Two biological trait categories found in large, long-lived organisms decreased with increasing temperature and decreasing precipitation at the most intermittent site. This result indicates that climate change might selectively affect taxa with certain traits. The robustness of the North Coast B-IBI and other common indices and metrics to temperature and precipitation variability demonstrates their continued applicability for examining water quality under future climate-change scenarios, but suggests that they probably will not be good indicators for detecting climate-change effects. The effects of climate change in mediterranean-climate streams can be monitored effectively within the framework of existing biological assessment programs by using regional indicators based on specific taxa identified to the generic level and information on their species traits.

Key words: climate change, mediterranean streams, benthic macroinvertebrates, biological assessment, climate indicators, B-IBI, species traits.

Long-term studies, particularly studies that span >10 y, are still relatively rare in freshwater ecology (Jackson and Füreder 2006), even though a long-term perspective is essential to understanding actual and potential impacts of climate change on community composition and structure in aquatic systems. Studies that span >10 y are particularly useful when examining the effects of long-term fluctuations in hydrology or temperature on macroinvertebrate communities (e.g., Bradt et al. 1999, Daufresne et al. 2004, Bêche and Resh 2007a, Ormerod and Durance 2009). Long-term studies also have established links between changes in macroinvertebrate communities and

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extreme climatic events (e.g., drought: Mouthon and Daufresne 2006, Bêche et al. 2009; freezing: Mulholland et al. 2009) and climatic cycles (North Atlantic Oscillation [NAO]: Bradley and Ormerod 2001, and El Niño Southern Oscillation [ENSO]: Bêche and Resh 2007b, Gilbert et al. 2008), both of which might increase in frequency under climate change (IPCC 2008).

Several studies from European temperate regions have demonstrated directional trends in community structure associated with increasing temperatures or climate-change-related shifts in stream flow (Daufresne et al. 2004, 2009, Burgmer et al. 2007, Durance and Ormerod 2007, 2009, Chessman 2009, Ormerod and Durance 2009). These shifts in community composition and structure are largely a result of selection toward temperature- or low-flow-tolerant species (Chessman 2009). Research examining the effects of climate change on species traits has focused primarily on individual taxonomic groups rather than entire communities (Mouthon and Daufresne 2006, Cordellier and Pfenninger 2008, Spooner and Vaughn 2008, Clausnitzer et al. 2009, Hering et al. 2009, Stamp et al. 2010). However, evidence exists that aquatic communities could experience dramatic shifts toward smaller size distributions with climate change, a pattern that has been shown for freshwater fishes and phytoplankton (Daufresne et al. 2009). This information brings into question the long-term applicability of newly established monitoring programs for local effects (e.g., urbanization and agriculture) because the metrics for reference sites (e.g., biotic indices) might be affected by climate change (Hamilton et al. 2010, Nichols et al. 2010). However, evidence from studies conducted in Europe suggests that biotic indices will be robust in the face of climate change, in that they will continue to be useful for detecting effects of the types of water pollution for which they were designed (Zamora-Muñoz et al. 1995, Morais et al. 2004, Leunda et al. 2009).

The implications of climate-change effects are region-specific in that the existing climate and the characteristics of its communities influence the potential responses to climate change (e.g., arctic ecosystems; Heino et al. 2009). Most climate-change research has been focused on temperate ecosystems, particularly in Europe (Rosenzweig et al. 2008), and research on aquatic macroinvertebrates is no exception to this pattern. In particular, little research has been done on potential climate-change effects in aquatic ecosystems in mediterranean-climate regions (MCRs). Bêche and Resh (2007a, b) and Bonada et al. (2007) have conducted studies suggesting that climate change might lead to greater changes in taxonomic composition than in biological traits (e.g., life-history traits and size) in MCRs. However, few studies have explicitly examined the effects of climate change (e.g., temperature increase) on benthic macroinvertebrates in these climatic regions (but see Feio et al. 2010).

Temperature and precipitation extremes over the past 20 y in the MCR of California have been analyzed using a range of time-series analyses. These extremes were determined, with high statistical confidence, to be outside of the range of natural variability (Bonfils et al. 2007, Maurer et al. 2007). Air temperatures in this region are expected to increase, on average, by an additional 1.5 to 4.5°C by 2100 (Cayan et al. 2009). Expectations for precipitation are more variable among existing models, but a drying tendency is expected in some locations (Cayan et al. 2009). Most General Circulation Models (GCMs) for California project greater warming in summer than in winter, most annual precipitation to continue to occur in winter, and possibly a longer rainy season with more sporadic individual rainfall events (Cayan et al. 2009). Most GCMs indicate that California will retain its characteristic mediterranean climate with relatively cool, wet winters and hot, dry summers.

Benthic macroinvertebrates are sensitive to changes in temperature, precipitation, and the associated flow regimes (Bunn and Arthington 2002, Lytle and Poff 2004), which should make them particularly responsive to the effects of climate change. For example, the anticipated increases in regional air temperatures, and consequently, water temperatures (Nelson and Palmer 2007), probably will affect benthic macroinvertebrates in MCR streams because temperature affects growth and timing of development and emergence (Bayoh and Lindsay 2003). Seasonal differences (rainy vs dry) in the abundance and composition of benthic macroinvertebrates in the MCR of California diminished during drought years and were correlated with patterns in ENSO, which are linked to temperature and precipitation (Bêche and Resh 2007b, Mazor et al. 2009). No evidence exists that the frequency or intensity of ENSO will increase because of climate change, but most GCMs indicate that ENSO will continue to influence climate patterns over the next century (Cayan et al. 2009). In addition, some metrics (e.g., taxon richness and Ephemeroptera, Plecoptera, Trichoptera [EPT] richness) are highly variable among years in coastal California streams, whereas others (e.g., Benthic Index of Biotic Integrity [B-IBI] and the ratio of observed to expected taxa [O/E] scores) are less variable (Mazor et al. 2009). The effects of climate change on these metrics and indices, on specific taxa, and on species traits have not been examined in detail in other studies.

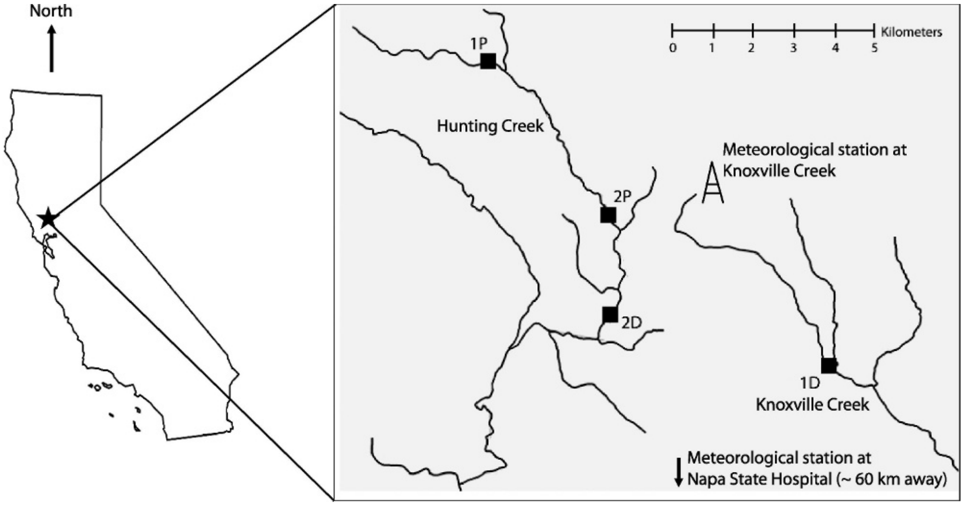

FIG. 1. Site map showing streams as black lines. Site 1D is on Hunting Creek, and sites 1P, 2P, and 2D are on Knoxville Creek.

Our objectives were to determine: 1) whether the core multimetric indicator of biological assessment programs in northern California (North Coast B-IBI; Rehn et al. 2005) will be robust against temperature and precipitation patterns associated with climate change, 2) whether commonly used metrics and indices are responsive to temperature and precipitation change (e.g., % EPT individuals, O/E scores); 3) whether taxon-based indicators that respond to climate change can be developed; and 4) whether a priori selected biological traits are responsive to climate change. These objectives have important implications for evaluating local landuse effects with biological monitoring programs in California because these programs are based on reference conditions, which might be affected by climate change. If so, multimetric indicators might have to be adjusted, e.g., by removing metrics sensitive to climate change, to detect reliably disturbances associated with land use. These implications of climate change also might be relevant to biological assessment programs in other MCRs worldwide, including areas in parts of Europe, southern California, South Africa, Australia, and Chile (Gasith and Resh 1999).

Methods

Study site and existing data

Our study is based on a 20-y, consistently collected benthic macroinvertebrate data set. Studies based on data sets of comparable duration have made important contributions to our understanding of climate-change effects (e.g., Perry et al. 2005, Both et al. 2006, Rosenzweig et al. 2008). Our data set might be particularly valuable because its length is comparable to most existing biological monitoring programs in the US (Resh and Rosenberg 1989, Jackson and Füreder 2006). Thus, the findings might apply directly to these programs. Our data set also is one of the most consistent data sets collected, in that benthic macroinvertebrates were sampled each year by the same individual (VHR), and identifications were done by the same individual (EPM). Each collection consisted of 5 Surber samples (0.093 m^2, 500-μm mesh), and all individuals in each sample were identified to genus or species (see Bêche et al. 2006 for additional detail).

The data set is composed of collections from 4 sites along 2 small, 1^{st}- and 2^{nd}-order, northern California streams, Knoxville and Hunting Creeks, in Lake County and Napa County, California (Fig. 1). The watersheds are relatively unaltered and are considered to represent reference conditions for small streams in the northern California MCR (see Bêche and Resh 2007a, b and Mazor et al. 2009 for further site details). Modest evidence exists that the benthic macroinvertebrate communities at the sites are relatively independent of each other and that the communities at the individual sites are correlated in time (Bêche and Resh 2007a, b). Sampling was done annually near 15 April from 1984 to 2003 at 3 of the sites (sites 1D, 2D, 2P), and from 1985 to 2003 at 1 of the sites (site 1P). The sampling date represents the end of the wet season, when most preemergence growth in all benthic macroinvertebrate orders occurs in this region (Mendez and Resh 2008). Samples were collected in a random design, stratified within riffles, and the same riffles were sampled each year. Two of the sampling sites are characterized by nonperennial flow (1D, 2D), and 2 are characterized by perennial flow (1P, 2P). Watershed areas range from ~2 to

~29 km^2, and the sites are all within a 500-m elevation range (Table 1).

Temperature and precipitation

Daily air temperature records were obtained from the meteorological station near Knoxville Creek within the University of California McLaughlin Nature Reserve (Fig. 1). These daily air temperature records covered the entire duration of the study except for the 1st y and some short gaps over the remaining years (<23 d). To create a complete daily data set for the study duration, daily air temperatures at Knoxville Creek were plotted against those at Napa State Hospital, which is ~60 km south of the study sites, and any missing values were calculated with the equation determined from a linear regression between the data from these 2 stations.

Daily air temperature records were used to calculate degree days (dd), which are correlated with insect development (Wilson and Barnett 1983). A threshold air temperature of 10°C was used as a baseline for calculating degree days because it is within the range of many macroinvertebrate species (Corkum 1992). The threshold temperature is the lower limit for invertebrate growth and development. A uniform value of the threshold temperature was used because our goal was only to distinguish warm years from cold years from the perspective of invertebrate development and not to elucidate distinct differences among the many aquatic species collected. The number of days that exceeded this threshold was calculated over the 15-wk period (January 1 to April 15) leading up to the sampling date.

Daily precipitation records were obtained from Napa State Hospital for the duration of the study. Complete records were unavailable from the closer meteorological station operated at the McLaughlin Reserve. The total amount of precipitation that occurred over the 15-wk period leading up to the sampling date was calculated to create a precipitation variable for analysis. To maintain consistency with the temperature analysis, the analysis was limited to the calendar year rather than to the start of the wet season in California, which typically occurs in October to early November, or to the water year, which begins October 1. The use of the calendar year is justified because new colonization of benthic macroinvertebrates is likely to occur throughout the duration of the wet season. Thus, starting at the beginning of the wet season is not crucial. Furthermore, years that are wetter on average in October through December tend to be wetter on average in January through April, and the same is true for temperature.

TABLE 1. Physical characteristics of the study sites.

Site	Stream	Stream order	Perenniality	Watershed area (km^2)	Latitude (N)	Longitude (W)	Elevation (m)	Stream width (m)
1D	Knoxville Creek	1	Nonperennial	2.1	38°47′56″	122°18′53″	390	3–8
2D	Hunting Creek	2	Nonperennial	22.1	38°48′30″	122°22′45″	402	10–15
1P	Hunting Creek	1	Perennial	4.4	38°51′56″	122°24′54″	634	5–10
2P	Hunting Creek	2	Perennial	29.3	38°49′45″	122°22′36″	348	10–15

Table 2. Years comprising the climate groups with degree days (dd) and total precipitation (mm) in parentheses.

Rank	Cool years	Warm years	Wet years	Dry years	Cool/wet years	Warm/dry years
1	1998 (14 dd)	1988 (66 dd)	1998 (68 mm)	1988 (15 mm)	1998 (14 dd, 68 mm)	1988 (66 dd, 15 mm)
2	1999 (18 dd)	1997 (53 dd)	1995 (68 mm)	1994 (17 mm)	1999 (18 dd, 47 mm)	1990 (49 dd, 22 mm)
3	1987 (32 dd)	1996 (51 dd)	1996 (58 mm)	2002 (20 mm)	2000 (32 dd, 47 mm)	1994 (46 dd, 17 mm)
4	2000 (32 dd)	1990 (49 dd)	2000 (47 mm)	1990 (22 mm)	1995 (35 dd, 68 mm)	1997 (53 dd, 30 mm)
5	1993 (33 dd)	1985 (47 dd)	1999 (47 mm)	1985 (23 mm)	1987 (32 dd, 33 mm)	1985 (47 dd, 23 mm)
6	1989 (34 dd)	1994 (46 dd)	1993 (44 mm)	1989 (25 mm)	1993 (33 dd, 44 mm)	2002 (40 dd, 20 mm)
7	1995 (35 dd)	1992 (45 dd)	1992 (37 mm)	1997 (30 mm)	1996 (51 dd, 58 mm)	2003 (44 dd, 35 mm)
Average	28 dd	51 dd	53 mm	22 mm	31 dd, 51 mm	49 dd, 23 mm

The relationship between air temperature (dd) and precipitation was examined using linear regression. A correlation between air temperature and precipitation could indicate synergistic effects between these variables. For example, high air temperatures could lead to low flows, which could lead to higher local water temperatures because of less thermal mass.

The years were ranked by number of degree days and by rainfall over the 15-wk period leading up to the sampling date. These rankings were used to establish 6 groups, each consisting of the 7 y at the extremes of the rankings: 1) cool vs warm, 2) wet vs dry, and 3) cool/wet vs warm/dry. Membership of years in groups was not exclusive (e.g., 1998 occurred in the cool group, the wet group, and the cool/wet group). The cool/wet and warm/dry groups were established by multiplying the rankings for temperature and precipitation to create a combined ranking that was used to sort years.

The 20 y in this data set were particularly dry compared to the past 50 y (Bêche et al. 2009), but each group was distinct (Table 2). The average degree days in cool years (28) was significantly different from warm years (51) ($p < 0.001$), and the average total precipitation in wet years (53 mm) was significantly different from dry years (22 mm) ($p < 0.001$). Therefore, we judged that interannual variability that occurred during the study period would be informative. At the very least, analyzing climate variability in the past would underestimate future climate changes, which are expected to be more extreme than those that have already occurred (IPCC 2008). The 3rd grouping, cool/wet vs warm/dry, was developed to determine if a synergistic effect between temperature and precipitation was evident in any of the metrics.

Macroinvertebrate analyses

Collection data.—The data from the 5 benthic macroinvertebrate samples for each collection event were combined by taking their average to avoid pseudoreplication in comparisons among sites. This composite data set was used to calculate a presence/absence matrix. Biological trait information was collected for nearly all of the taxa in the data set from a variety of published sources (see Bêche et al. 2006, Bêche and Resh 2007b for methods). The data consisted of 206 taxa and 146,697 individuals comprising 79 families and 24 orders. However, converting these taxa to operational taxonomic units (OTUs) for metric calculation reduced the number of taxa to 137 OTUs. This reduction was primarily a result of aggregation of Chironomidae to family and elimination of semiaquatic Hemiptera. Converting these taxa for calculation of the O/E calculation further reduced the number to 125 OTUs for the O/E analyses.

Independence among sites was examined using nonmetric multidimensional scaling analysis (NMDS) on the $\log_{10}(x + 1)$-transformed taxon abundances of all taxa. PC-ORD 4.27 software (MjM Software Design, Gleneden Beach, Oregon) was used to obtain a 2-dimensional solution based on Sørenson distance (McCune and Mefford 1999). Clustering among the sites in ordination space was examined in relation to the categorical variables, stream order, and perenniality. The NMDS was run with 2 axes, 10 runs with real data, a stability criterion of 0.006, 50 iterations to evaluate stability, and a maximum number of iterations of 100.

Biological metrics evaluated for robustness to climate change.—The North Coast B-IBI is a multimetric index developed for water-quality monitoring in northern California (Rehn et al. 2005) and is used in California by state agencies to evaluate local anthropogenic stresses on stream communities (Rehn et al. 2007). The 8 metrics that comprise the North Coast B-IBI are: EPT richness, Coleoptera richness, Diptera richness, % intolerant individuals, % nongastropod scraper individuals, % predators, % shredder taxa, and % noninsect taxa. These metrics were calculated from the data with a Monte Carlo simulation without replacement to standardize sample size to 500 individuals, as required by the North Coast B-IBI (Rehn et al. 2005). For each site, the response of these metrics to both degree days and total precipitation (for the 15-wk period prior to sampling) was determined with linear regression. In addition, Student's *t*-tests were used to compare the average North Coast B-IBI value between the a priori groupings (e.g., cool vs warm, wet vs dry, and cool/wet vs warm/dry) to determine whether the North Coast B-IBI could be used as an indicator of climate change for this locality.

Several other widely used indices and metrics were evaluated to determine if they were responsive to temperature and precipitation change: % EPT individuals, total richness, and EPT richness divided by Odonata, Coleoptera, Hemiptera richness (EPT/OCH; Bonada et al. 2006). The O/E(50) was calculated from a River Invertebrate Prediction and Classification System (RIVPACS)-type model developed for California (see Ode et al. 2008 for details). O/E(50) includes only the common species found at >50% of reference sites. Each metric and index was plotted against degree days and precipitation and fit with linear regression. Student's *t*-tests were used to compare values for cool vs warm years, wet vs dry years, and cool/wet vs warm/dry years. A *p*-value of 0.2 was selected as a threshold of significance to reduce the probability of false negatives (Type II error) for marginally affected metrics. No metric was strongly affected. Our analysis was primarily exploratory and was not intended to establish significance rigorously, so Bonferroni corrections were not made.

Local climate-change indicator.—The final climate-change indicator was based on annual presence/absence data from the taxa observed at all 4 sites. Annual presence/absence gave equal weight to taxa that were less common. To construct the final indicator, individual temperature (warm vs cool) and precipitation (dry vs wet) indicators (hereafter, preliminary temperature and precipitation indicators) were developed from the data set with an iterative process that used only a random subset of the data. For example, the 1st iteration of the preliminary temperature indicator used 6 of the 7 y that fit the warm and cool criteria, respectively. Within the warm group, 6 y of data at 4 sites yielded a total of 24 sampling events for screening. The year that was randomly withheld from the 7 y in each group for each iteration was used for internal validation and for consideration of taxa for inclusion in the final climate-change indicator as discussed below.

All taxa were screened to determine which were more common in the warm than in the cool group by ≥8 of 24 sampling events (a difference of 33%). For example, if a given taxon was present at 12 sampling events during the warm years of 1 iteration, and 4 sampling events during the cool years, it would be selected for inclusion in this iteration. The total number of taxa selected by this process was calculated for each iteration. For example, in the 1st iteration, 12 taxa showed a positive affinity with warm years. The next step was to determine the presence of these taxa at each individual site–year combination, which was recorded as the proportion present out of those 12. Thus, 24 different proportions/iteration were calculated from these 6 y of data (4 sites/y). The mean and standard error of this proportion were calculated, and a *t*-test was used to compare the preliminary temperature indicator between warm years (8.2/12) and cool (3.3/12) years in our 1st-iteration example.

Internal validation was completed simultaneously with the taxon-screening process. For example, in the 1st iteration for the cool vs warm comparison, the preliminary temperature indicator was composed of 12 taxa. The next step was to determine the presence of these taxa at each site in the data for the year that was withheld for internal validation. The proportion present of those 12 taxa was recorded. Therefore, 4 different proportions/iteration were calculated from this 1 y of validation data. A *t*-test was used to compare the preliminary temperature indicator between warm (7.3/12) and cool (7.8/12) years in our 1st iteration example. When the result was significant, the taxa in that iteration were each given a point and considered for the final indicator. The total number of significant comparisons among the iterations of this internal validation was compared against the total number of significant comparisons from the 6 y that were used to select the taxa to assess the validity of the approach.

This iteration process was completed 10 times for the wet vs dry groups and 10 times for the cool vs warm groups. To determine which taxa to include in the final climate-change indicator, which represented a combination of temperature and precipitation effects, a criterion for taxa was set that resulted in significant *t*-tests between groups in the internal validation on ≥4 of 20 possible comparisons (e.g., the taxa had ≥4 points). For example, the caddisfly genus *Hydroptilia*, which was included in the final indicator, was involved in 5 of 5 significant temperature models and 2 of 5 significant precipitation models, and, therefore, was significant on 7 occasions. The goal for selecting taxa from the significant comparisons in the internal validation was to reduce the limitations of fitting the model to the specific years of the study. Last, the proportional value of the final climate-change indicator was transformed to a 10-point scale to make the indicator values easier to compare on a linear scale.

An external validation was done on the final climate-change indicator to reduce the limitations of fitting the model to the specific sites of the study. This external validation was accomplished with a data set of 47 individual sampling events made at 40 reference sites from 2000 to 2007 across the greater San Francisco Bay area. Benthic macroinvertebrates in this data set were collected with a targeted-riffle sampling method (Barbour et al. 1999). Most sites were sampled by personnel from the San Francisco Regional Water Quality Control Board through the Surface Water Ambient Monitoring Program (SWAMP). Additional sites were sampled by personnel from the Alameda Countywide Clean Water Program, Contra Costa Clean Water Program, Marin County Stormwater Pollution Prevention Program, San Mateo Countywide Water Pollution Prevention Program, Santa Clara Valley Urban Runoff Pollution Prevention Program, Sonoma Ecology Center, and the Institute for Conservation Advocacy Research and Education.

To test the indicator on the external data set, the 2 wettest years (2005, 2006) and 2 driest years (2001, 2007) were selected from this 8-y period. The mean and standard error of the climate-change indicator were calculated for each precipitation group (wet and dry) with the final taxa that were selected for the indicator from the 20-y study data set. These values were compared (wet vs dry years) with a *t*-test. If the values were significantly different, the external validation was deemed successful.

Last, the value of the final climate-change indicator was calculated for the original groups containing 7 y of data for each site (cool vs warm, wet vs dry, and cool/wet vs warm/dry). The mean and standard error were calculated for each group, and differences between groups were evaluated with a *t*-test.

Biological traits.—Three biological traits (voltinism, maximum body size, and desiccation resistance) were hypothesized a priori to be sensitive to temperature or precipitation based on their functional attributes (Bêche et al. 2006, Bonada et al. 2007). We focused on specific categories within these traits (semivoltine life cycle, maximum body size >40 mm, and desiccation resistance) that probably would respond to climate-change effects.

The distribution of biological traits among taxa was calculated from the presence–absence matrix instead of the abundance data because some taxa with these traits tend to be rare in the community. The traits for all taxa present in each sample and the proportional representation of each trait category were determined. The fuzzy coding approach was used (Chevenet et al. 1994), so each taxon could be described by a fractional composition of multiple trait categories (where the fractions sum to 1), e.g., a taxon could be described as 0.4 semivoltine and 0.6 bivoltine, which would indicate that this taxon has partial semivoltine and partial bivoltine characteristics.

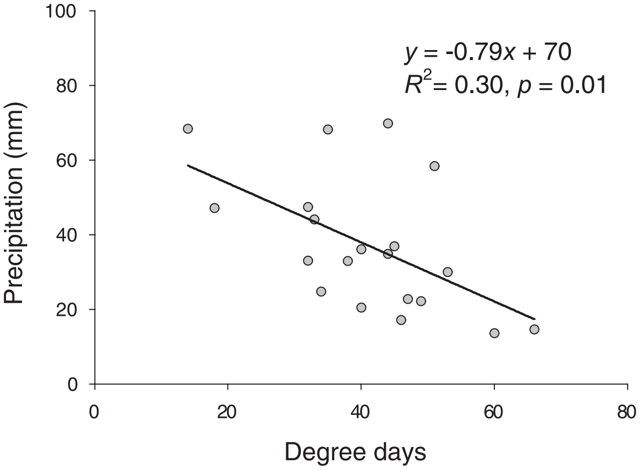

FIG. 2. Linear regression of total precipitation against degree days, both calculated from the 15-wk period (January 1–April 15) leading up to the sampling date.

Results

Physical conditions

The daily average air temperatures measured at Knoxville Creek were linearly related ($R^2 = 0.78$) to those measured at Napa State Hospital ($y = 1.3x - 4.5$). Therefore, air temperatures and the degree days calculated for the sites were assumed to be comparable at each site. Degree days and precipitation from January 1 to April 15 were highly variable from year to year. Degree days ranged from a minimum of 14 in 1998 to a maximum of 66 in 1988, a 5× difference. Precipitation ranged from 15 cm in 1988 to 68 cm in 1995 and 1998, a 5× difference. This high interannual variability is evident among the temperature and precipitation values characterizing the different year groups (Table 2).

Degree days and precipitation were inversely related ($R^2 = 0.30$, $p = 0.01$; Fig. 2) within the study area. Cool years were more likely to be wet, and warm years were more likely to be dry. This pattern explains the similarity in the years included in the cool and wet groups and in the years included in the dry and warm groups. However, the low R^2 indicates that the effects of temperature and precipitation should not be treated as a single variable.

The NMDS plot revealed distinct clusters of 1st- and 2nd-order sites (Fig. 3A) and of nonperennial and perennial sites (Fig. 3B). This result indicates that the

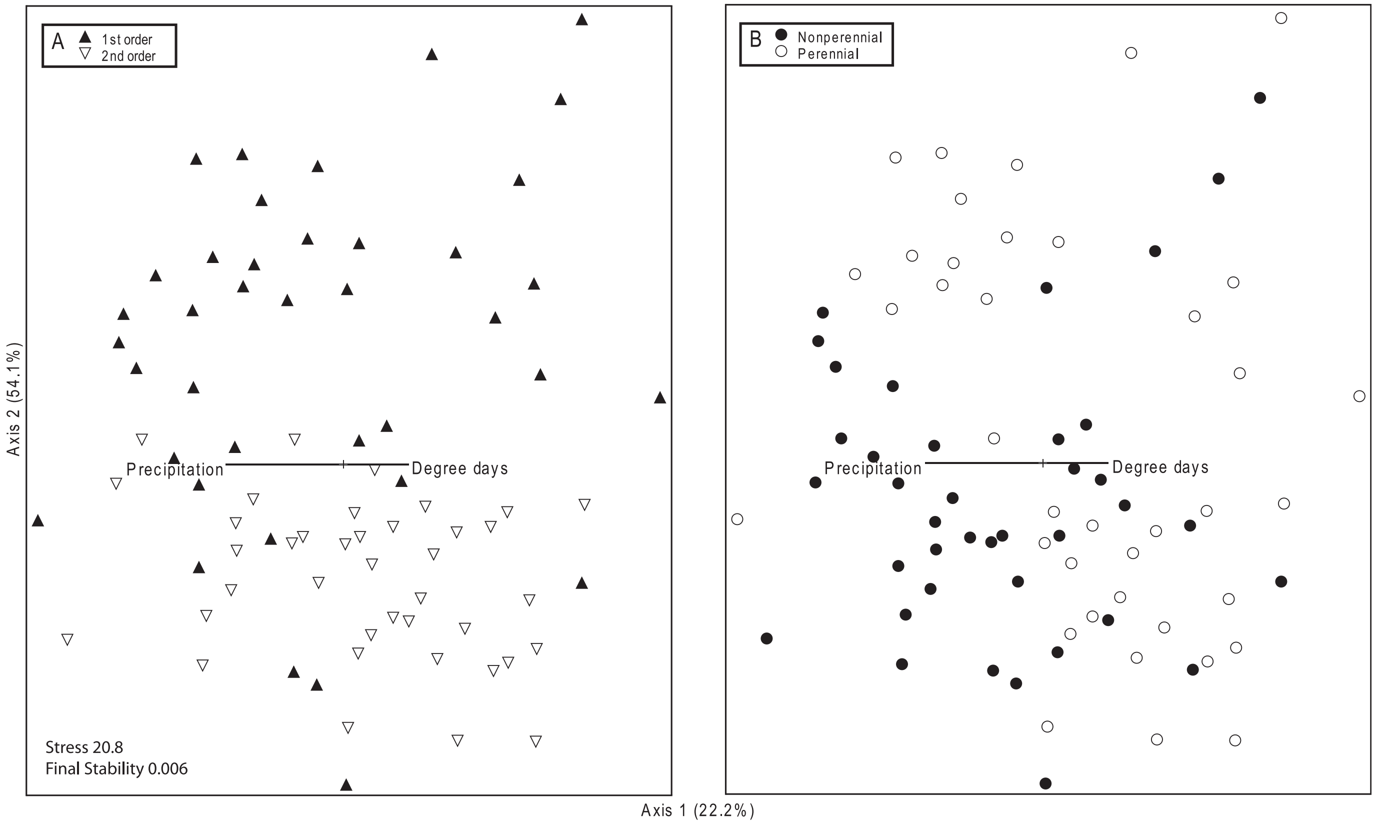

FIG. 3. Clustering of taxa using 2-dimensional nonmetric multidimensional scaling analysis with axis 1 aligned with degree days and sites coded by stream order (A) and perenniality (B). The lengths of the line segments extending from the vertical mark at the center of axis 1 are proportional to the amount of variability in benthic community structure that is explained by precipitation (extending to the left) and degree days (extending to the right).

benthic macroinvertebrate communities at each site were independent to some extent, despite being within the same watershed. The 1st axis on the NMDS plot was correlated with degree days ($R^2 = 0.22$) and precipitation ($R^2 = 0.31$). Degree days and precipitation were aligned in opposite directions, indicating a strong, negative correlation within ordination space (Fig. 3A, B).

Biological metrics

The North Coast B-IBI did not change significantly with temperature and precipitation at any site (Fig. 4A–H). However, the low power of the test ($\beta < 0.8$ in each case) indicates a limited ability to detect a difference. Furthermore, the North Coast B-IBI did not differ significantly between cool and warm or wet and dry years (Table 3). The only significant ($p \leq 0.05$) regressions among the 8 component metrics of the North Coast B-IBI were Coleoptera richness against degree days at site 1P (Table 4), Coleoptera richness against precipitation at site 1D (Table 5), and % shredder taxa at site 1D (Table 5). In the regressions of metrics against degree days, Coleoptera richness, % intolerant individuals, % nongastropoda scraper individuals, and % noninsect taxa had regressions with p-values ≤ 0.2. In the regressions of metrics against precipitation, EPT richness, Coleoptera richness, % intolerant individuals, % predators, and % shredder taxa had regressions with p-values ≤ 0.2. Coleoptera richness and % intolerant individuals were correlated with both degree days and precipitation, results suggesting that these 2 metrics might be the most responsive to climate change. However, the direction of the Coleoptera richness responses differed between sites 1D and 2D.

Most of the other indices and metrics were not responsive to temperature or precipitation fluctuations. The average values of O/E(50), % EPT individuals, and total richness showed no substantial trends with climate (Table 3). EPT/OCH showed the greatest association with climate, but the direction was not consistent between wet and dry years.

Local climate-change indicator.—Differences in taxon occurrences between groups (warm vs cold and wet

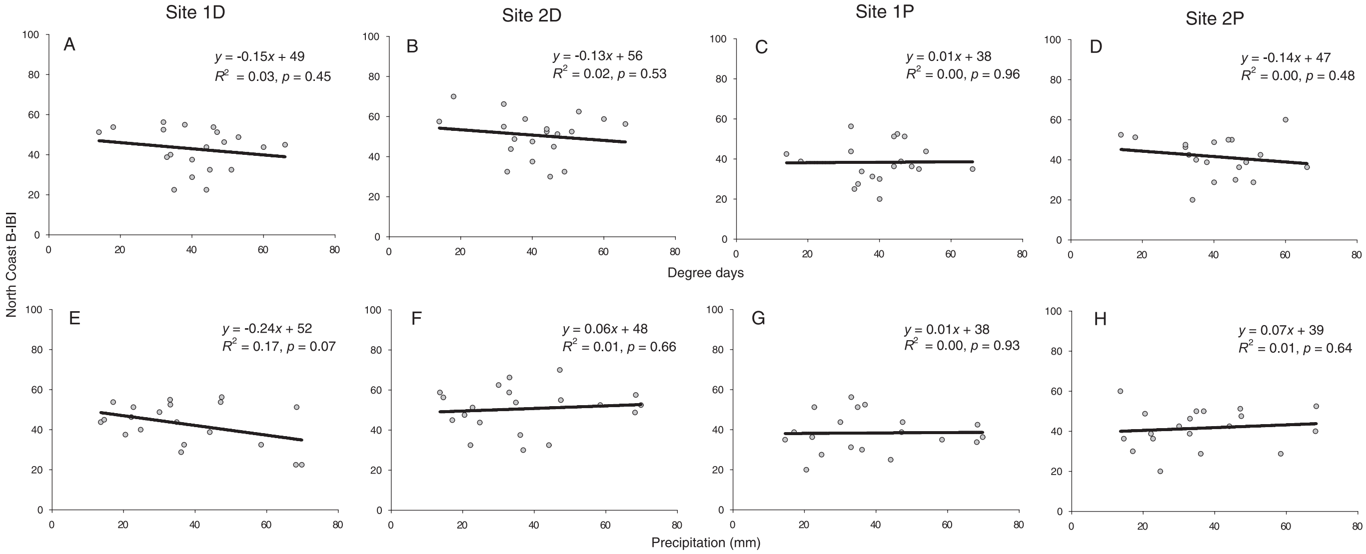

FIG. 4. The North Coast Benthic Index of Biotic Integrity (B-IBI) plotted against degree days and precipitation at sites 1D (A, E), 2D (B, F), 1P (C, G), and 2P (D, H) and fit with linear regression trend lines.

vs dry) ranged from 0 to 15 in most iterations and were close to 0 for most of the 206 total taxa. A difference of ≥8 was the criterion for inclusion in the preliminary temperature and precipitation indicators. In the 20 iterations, the preliminary indicators detected a significant difference ($p < 0.05$) between groups (cool vs warm and wet vs dry) in all of the groups containing the 6 y of data from which the indicators were constructed. In these same 20 iterations, the preliminary indicators detected a significant difference between groups in ½ of the cool vs warm groups (iterations 1, 2, 5, 6, and 10) and ½ of the wet vs dry groups (iterations 1, 3, 6, 7, and 9) that contained the 1 y of data withheld for internal validation purposes. Thus, internal validation indicated that this method adequately selected taxa 50% of the time.

Of the 13 total genera selected as preliminary indicator taxa during the iterations (Table 6), 9 were ultimately selected to comprise the final climate-change indicator because they were present in ≥3 of the 20 iterations in the internal validation. The taxa that comprised the final indicator were *Ambrysus* (Hemiptera), *Chironomidae* (Diptera), *Dixa* (Diptera), *Euparyphus* (Diptera), *Hydropsyche* (Trichoptera), *Hydroptilia* (Trichoptera), *Lepidostoma* (Trichoptera), *Ochrotrichia* (Trichoptera), and *Trichocorixa* (Hemiptera). These taxa are in 3 orders: Trichoptera (n = 4), Diptera (n = 3), and Hemiptera (n = 2). Trichopterans made up 23% of the overall taxon list and 44% of the taxa in the indicator (i.e., 4 of the 9 taxa selected), so it is unlikely that their high representation in the indicator is entirely the result of chance. The difference in the number of years of presence of these taxa between the cool and wet and the warm and dry groups ranged from 5 to 14 (Table 7).

The final climate-change indicator was able to detect a significant difference between year groups (warm vs cool, wet vs dry, cool/wet vs warm/dry) in 10 of the 12 comparisons examined (Table 8). The difference in the average indicator value for all the sites combined was highest between the dry and wet years (6.8 − 2.7 = 4.1). The difference between the cool and warm years and the cool/wet and warm/dry years was 2.8 in each case. This result agrees with the NMDS ordination (Fig. 3A, B) of the raw abundance data for all taxa, which showed that precipitation was a stronger driver than temperature in shaping patterns in the benthic community, as indicated by the length of the vector. The difference in the average indicator value between groups was typically larger in the nonperennial sites than in the perennial sites.

The final climate-change indicator (developed with long-term data from 4 study sites in 2 streams) was robust when used with the external validation (regional) data set from 47 sampling events at 40 sites from throughout the greater San Francisco Bay area. The indicator values differed by 0.8 units between wet years (indicator value = 1.9) and dry years (indicator value = 2.8). This difference was smaller than that observed in the local data set (i.e., 2.8), but it was statistically significant (p = 0.001). All but 1 of the 9 taxa were prevalent in both the local and regional data set. The exception was *Ambrysus*.

TABLE 3. Mean (SE) metric and index values between cool and warm years, wet and dry years, and cool/wet and warm/dry years. B-IBI = benthic index of biotic integrity; O/E(50) = ratio of observed to expected taxa including only the common species found at >50% of reference sites; EPT = Ephemeroptera, Plecoptera, Trichoptera; OCH = Odonata, Coleoptera, Hemiptera. * indicates comparisons considered to be marginally affected by climate change ($p \leq 0.20$).

		Temperature			Precipitation			Temperature/precipitation		
Metric	Site	Cool years	Warm years	*p*	Wet years	Dry years	*p*	Cool/wet years	Warm/dry years	*p*
North Coast B-IBI	1D	39 (4.4)	45 (2.7)	0.25	40 (5.5)	45 (2.2)	0.35	42 (7.2)	47 (2.5)	0.48
	2D	47 (5.5)	53 (2.6)	0.37	53 (4.2)	48 (3.3)	0.39	52 (7.9)	51 (3.0)	0.88
	1P	39 (3.9)	38 (2.8)	0.86	36 (2.4)	36 (3.9)	0.94	35 (3.8)	38 (5.0)	0.63
	2P	45 (3.2)	36 (4.8)	0.16*	45 (3.2)	39 (4.9)	0.32	47 (3.1)	37 (6.6)	0.25
O/E(50)	1D	0.30 (0.031)	0.34 (0.028)	0.45	0.30 (0.041)	0.32 (0.023)	0.59	0.30 (0.049)	0.32 (0.032)	0.69
	2D	0.46 (0.038)	0.55 (0.052)	0.21	0.50 (0.048)	0.46 (0.055)	0.53	0.66 (0.46)	0.50 (0.062)	0.69
	1P	0.25 (0.022)	0.26 (0.014)	0.59	0.25 (0.022)	0.28 (0.010)	0.26	0.23 (0.031)	0.28 (0.01)	0.19*
	2P	0.30 (0.049)	0.40 (0.016)	0.08*	0.30 (0.049)	0.42 (0.038)	0.08*	0.28 (0.089)	0.42 (0.054)	0.23
% EPT individuals	1D	29 (9.1)	43 (7.7)	0.25	37 (8.0)	43 (9.0)	0.62	23 (6.6)	42 (11)	0.21
	2D	49 (2.5)	44 (3.4)	0.28	48 (2.8)	47 (3.9)	0.84	53 (2.0)	43 (3.8)	0.07*
	1P	19 (7.3)	19 (5.0)	0.98	19 (7.3)	21 (5.8)	0.88	17 (13)	21 (7.7)	0.80
	2P	39 (11)	51 (9.5)	0.42	34 (8.8)	47 (8.3)	0.28	38 (15)	45 (10)	0.72
Total richness	1D	21 (3.0)	23 (1.6)	0.48	20 (2.7)	21 (2.8)	0.86	17 (4.1)	23 (2.3)	0.21
	2D	28 (2.1)	25 (2.9)	0.46	24 (1.9)	27 (2.4)	0.41	25 (1.9)	28 (3.2)	0.50
	1P	21 (1.5)	21 (1.5)	0.90	19 (1.5)	20 (1.5)	0.79	20 (2.1)	22 (2.4)	0.60
	2P	19 (0.84)	22 (2.36)	0.18*	4.2 (1.3)	2.7 (0.19)	0.27	16 (3.1)	23 (1.0)	0.05*
EPT richness/OCH richness	1D	3.61 (0.75)	2.91 (0.85)	0.55	4.02 (0.97)	2.64 (0.65)	0.26	4.2 (1.0)	2.1 (.12)	0.05*
	2D	4.37 (0.53)	4.21 (1.16)	0.90	2.4 (0.23)	3.2 (0.38)	0.09*	2.7 (0.29)	2.8 (0.19)	0.80
	1P	2.87 (0.48)	1.53 (0.25)	0.03*	2.7 (0.35)	1.8 (0.38)	0.13*	2.8 (0.35)	1.6 (0.47)	0.09*
	2P	2.90 (0.19)	2.53 (0.23)	0.23	23 (0.98)	19 (2.6)	0.15*	3.5 (1.2)	2.8 (0.22)	0.55

TABLE 4. Linear regression statistics for the component metrics of the North Coast Benthic Index of Biotic Integrity (B-IBI) vs degree days. EPT = Ephemeroptera, Plecoptera, Trichoptera. * indicates trends with increasing temperature considered to be marginally affected by climate change ($p \leq 0.20$).

	Site 1D			Site 2D			Site 1P			Site 2P		
Regression variable	R^2	p	Trend	R^2	p	Trend	R^2	p	Trend	R^2	p	Trend
EPT richness	0.01	0.70		0.00	0.81		0.02	0.60		0.01	0.67	
Coleoptera richness	0.15	0.09*	Increase	0.01	0.76		0.24	0.03*	Increase	0.01	0.68	
Diptera richness	0.04	0.41		0.06	0.29		0.04	0.39		0.00	0.89	
% intolerant individuals	0.01	0.75		0.11	0.15*	Decrease	0.00	0.86		0.024	0.51	
% nongastropod scraper individuals	0.00	0.90		0.01	0.68		0.10	0.18*	Increase	0.024	0.51	
% predators	0.09	0.70		0.02	0.56		0.01	0.71		0.031	0.46	
% shredder taxa	0.07	0.26		0.06	0.29		0.16	0.09*	Decrease	0.022	0.53	
% noninsect taxa	0.01	0.74		0.10	0.18*	Decrease	0.02	0.56		0.00	0.78	

Biological traits

Two of the 3 selected traits showed consistent trends between cool vs warm years and wet vs dry years. However, these trends were statistically significant only at the site with the most extreme conditions of intermittency, i.e., the 1st-order, nonperennial (1D) site (Fig. 5A–D). The trends included a decrease in macroinvertebrates with a life cycle >1 y and a decrease in macroinvertebrates with a body size >40 mm with increasing temperature or with decreasing precipitation. Desiccation resistance, which was hypothesized to be potentially responsive to temperature, did not differ consistently or significantly among sites.

Cool/wet vs warm/dry years

Metrics and indices did not differ more strongly between cool/wet years and warm/dry years, which represent the strongest combination of climate change effects examined, than between wet and dry or cool and warm years. However, the difference in total richness between cool/wet years and warm/dry years was statistically significant at 1 of the sites (2P), whereas it was not significant for any of the individual temperature or precipitation comparisons (Table 3).

Discussion

The high interannual variability in temperature and precipitation that was observed among years in our study is characteristic of MCRs worldwide (Gasith and Resh 1999). This variability is related to the ENSO weather phenomenon through complex relationships that are region specific (Brönnimann et al. 2007). In the MCR of Europe, for example, the ENSO is nonlinearly associated with winter precipitation anomalies (Pozo-Vázquez et al. 2005). In the MCR of southern California, El Niño winters tend to be wetter than normal (Cayan et al. 2009), but the pattern is not as clear in northern California. Worldwide, the ENSO has played a key role in shaping patterns of climate

TABLE 5. Linear regression statistics for the component metrics of the North Coast Benthic Index of Biotic Integrity (B-IBI) vs precipitation. EPT = Ephemeroptera, Plecoptera, Trichoptera. * indicates trends with increasing precipitation considered to be marginally affected by climate change ($p \leq 0.20$).

	Site 1D			Site 2D			Site 1P			Site 2P		
Regression variable	R^2	p	Trend	R^2	p	Trend	R^2	p	Trend	R^2	p	Trend
EPT richness	0.13	0.11*	Decrease	0.06	0.32		0.01	0.69		0.00	0.87	
Coleoptera richness	0.25	0.03*	Decrease	0.09	0.19*	Increase	0.00	0.92		0.064	0.30	
Diptera richness	0.00	0.82		0.05	0.37		0.01	0.68		0.020	0.57	
% intolerant individuals	0.08	0.23		0.01	0.71		0.14	0.12*	Increase	0.01	0.71	
% nongastropod scraper individuals	0.01	0.67		0.00	0.99		0.00	0.97		0.00	0.79	
% predators	0.03	0.46		0.00	0.92		0.18	0.07*	Increase	0.06	0.32	
% shredder taxa	0.07	0.01*	Decrease	0.15	0.09*	Increase	0.03	0.48		0.01	0.74	
% noninsect taxa	0.00	0.96		0.07	0.27		0.00	0.83		0.00	0.95	

TABLE 6. Taxa considered for inclusion in the final climate-change indicator because they were present in ≥1 of the internal validation iterations that detected a significant difference between groups (i.e., cool vs warm, wet vs dry). The taxa included in the final indicator are marked with an * and were selected based on having ≥3 points (occurrence sums across rows). I = iteration.

Taxa	Cool years vs warm years					Dry years vs wet years					Occurrences (points)
	I 1	I 2	I 5	I 6	I 10	I 1	I 3	I 6	I 7	I 9	
Euparyphus (Diptera)*	Present	Present	Present	Present	Present	Present	Present	Present	Present	Present	10
Hydroptilia (Trichoptera)*	Present	Present	Present	Present	Present	Present	Present	Present	Present		9
Dixa (Diptera)*	Present	Present	Present		Present	Present	Present	Present	Present	Present	9
Hydropsyche (Trichoptera)*	Present	Present	Present	Present	Present	Present			Present		7
Ochrotrichia (Trichoptera)*	Present	Present				Present	Present		Present		5
Ambrysus (Hemiptera)*	Present	Present		Present	Present						4
Chironomidae (Diptera)*	Present	Present				Present			Present		4
Lepidostoma (Trichoptera)*		Present			Present					Present	3
Trichocorixa (Hemiptera)*						Present		Present		Present	3
Tipula (Diptera)							Present			Present	2
Tropisternus (Coleoptera)	Present			Present							2
Oreodytes (Coleoptera)	Present		Present								2
Planariidae (Seriata)	Present										1

variability in MCRs over the past millennium (Mann 2006).

The significant inverse correlation between temperature and precipitation illustrates that the effects observed in our study could be related to either or both of these variables. Correlations between regional air temperatures and precipitation have been observed in other MCRs (e.g., Milly et al. 2005, Chu et al. 2008). However, the mechanism of influence from temperature might not be direct. For example, water temperature is inversely correlated with dissolved O_2 levels in streams and rivers, which can affect benthic macroinvertebrates (Morrill et al. 2005, Jacobsen and Marín 2007). In addition, the mechanism of the effect of dissolved O_2 on benthic macroinvertebrates could be related to other unmeasured explanatory variables, such as amount of canopy cover or groundwater input. These mechanisms could not be tested directly because year-to-year variability of these variables was not measured.

The benthic macroinvertebrate communities observed in the perennial and nonperennial and in the 1st- and 2nd-order sites were different, a result that is in agreement with the findings in Bêche and Resh (2007a, b), Bêche et al. (2009), and Mazor et al. (2009). Perenniality and stream order also shape distinct benthic communities in the MCRs of Europe (e.g., Bonada et al. 2007, Anna et al. 2009, Feio et al. 2010) and California (e.g., Bonada et al. 2006, Bêche et al. 2006, Bêche and Resh 2007b, Mazor et al. 2009). One of the key findings of our study was that the greatest association between biological traits and climate occurred in the 1st-order, nonperennial site 1D, probably because it represents the most extreme, intermittent conditions. The longer-lived (life cycle > 1 y), larger (maximum body size > 40 mm) organisms at this site were clearly less abundant in warmer and drier years, probably because of their lower tolerance to extreme conditions.

Some of the most widely used biological metrics (e.g., % EPT, total richness) and local indices (e.g., the North Coast B-IBI) were robust against interannual changes in temperature and precipitation, so these metrics should have continued usefulness for biological assessment programs aimed at detecting local anthropogenic stressors under climate-change scenarios. However, the low power ($\beta < 0.8$) indicates that these findings should be interpreted cautiously. The values of the B-IBI and % EPT were low relative to values typically observed in reference sites in other parts of northern California outside the MCR. This difference is related to the stresses in the MCR, i.e., floods followed by drying, which are the reference conditions in this region. A fairly constant %

TABLE 7. Number of times (in 28 sampling events) that the component taxon was present in cool/wet years (7 y total) and warm/dry years (7 y total) and the absolute difference between the year groups for the final climate-change indicator.

Genus (Order)	Cool/wet years	Warm/dry years	Difference (|cool/wet – warm/dry|)
Ambrysus (Hemiptera)	4	10	6
Chironomidae (Diptera)	14	21	7
Dixa (Diptera)	6	20	14
Euparyphus (Diptera)	12	20	8
Hydropsyche (Trichoptera)	13	18	5
Hydroptilia (Trichoptera)	8	16	8
Lepidostoma (Trichoptera)	5	13	8
Ochrotrichia (Trichoptera)	17	25	8
Trichocorixa (Hemiptera)	9	16	7

composition of the same dominant taxa was observed among the years, and this result indicates that the foundation of the benthic community might remain intact despite temperature and precipitation changes. This apparent resilience might be related to the unpolluted nature of these sites and to the severe conditions, i.e., sequential flooding and drying, of the mediterranean climate itself (Gasith and Resh 1999), which selects highly resilient organisms. For example, an unpolluted site would tend to have a higher EPT/OCH because of the higher EPT composition. However, an unpolluted site also could have low EPT/OCH if riffles are relatively less common than pools in the system (Bonada et al. 2006). EPT/OCH was lower in the warm than in the cold years at all sites and lower in the dry than in the wet years in 3 of the 4 sites although not all of these differences were statistically significant. A combination of polluted water and increasing temperature might have a compounded, negative effect on metrics based on the OCH orders, and this possibility should be tested further.

The North Coast B-IBI and other commonly used metrics and indices might be unresponsive to the expected climate-change scenarios because many of the component metrics are calculated for taxa identified at the order level. Genera might come and go, but if replacement occurs, order-level metrics would be unchanged. However, some specific macroinvertebrate genera did appear to be consistently responsive to climate changes, and these taxa were the ones that we incorporated into the climate-change indicator. The functionality of the indicator might result from its ability to account for generic-level turnover, because it is based on individual taxa. These taxa, which were primarily trichopterans, might be among the most susceptible to climate change and could be useful components to include in biological-monitoring programs aimed at detecting climate-change effects.

The debate about the general usefulness of higher (e.g., order and family) compared to lower (e.g., genus and species) levels of taxonomic resolution for evaluating anthropogenic changes has gone on for decades (e.g., Resh and Unzicker 1975). Lenat and Resh (2001) provide many examples of when species or generic levels might be more useful than higher levels. The potential usefulness of generic-level indicators for detecting climate change, which was a key finding of our study, suggests that this result should be added to that list.

Modest evidence was found for a filtering effect on biological traits at the site with the most extreme conditions of intermittency. This result indicates that

TABLE 8. Mean (SE) value of the local climate-change indicator in the different year groups. * indicates significant comparisons ($p < 0.05$).

	Temperature			Precipitation			Temperature/precipitation		
Site	Cool years	Warm years	p	Wet years	Dry years	p	Cool/wet years	Warm/dry years	p
1D	3.8 (0.9)	6.2 (0.9)	0.05*	1.1 (0.7)	6.5 (0.3)	0.004*	3.5 (0.9)	6.0 (0.7)	0.05*
2D	2.2 (0.9)	6.5 (0.8)	0.005*	1.9 (0.7)	7.0 (0.5)	<0.001*	1.9 (0.8)	6.8 (0.7)	<0.001*
1P	4.0 (0.8)	6.2 (0.8)	0.01*	3.8 (0.7)	6.0 (0.4)	0.038*	4.1 (0.8)	5.4 (0.9)	0.3
2P	4.9 (1.0)	7.0 (0.9)	0.10	4.0 (0.6)	7.5 (0.6)	0.003*	4.4 (0.9)	7.0 (0.8)	0.05*
Average	3.7	6.5		2.7	6.8		3.5	6.3	

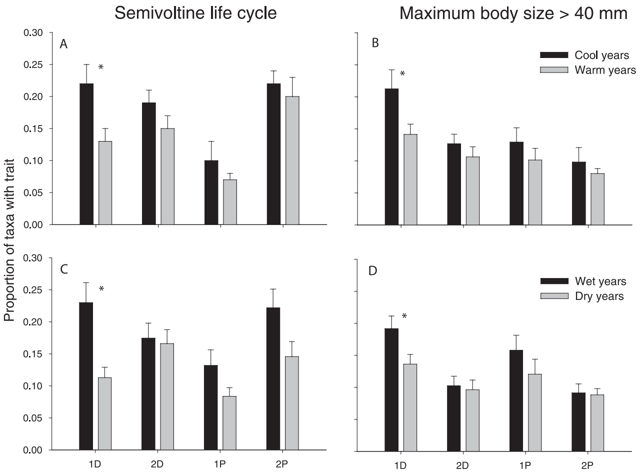

FIG. 5. Mean (±1 SE) proportion of taxa with semivoltine life cycles (A, C) and maximum body size >40 mm (B, D) at the study sites in cool and warm years (A, B) and wet and dry years (C, D). * indicates a significant difference ($\alpha = 0.05$) between groups of years (Student's *t*-test).

the benthic communities in intermittent habitats might experience the strongest selective force under the expected conditions of climate change. Our study also illustrates the usefulness of a priori hypothesis testing based on specific trait categories, which thus far, is not a widely used approach in trait studies on North American freshwater macroinvertebrates. The prevalence of specific biological traits (i.e., voltinism and maximum body size) differed significantly between cool and warm years and between wet and dry years at the most intermittent site, but any evolutionary response would occur over a much longer time period. Several studies conducted in MCRs have found that traits are less sensitive to climate change than are taxonomic composition and abundance measures (e.g., Bêche et al. 2006, Bêche and Resh 2007b, Bonada et al. 2007). However, the sensitivity of species traits might depend on the extremeness or severity of changes at a site, which tend to be highest in 1^{st}-order, nonperennial streams and is compounded in streams without riparian cover.

A presence-based climate-change indicator appears to be useful for evaluating the effects of future climate change at the specific sites used in our study. Such an indicator also might be applicable at a regional scale, as evidenced by the successful external validation at sites throughout the San Francisco Bay area. However, the strength of the climate signal was lower between groups in the regional data set than in the local data set. The reduced signal strength in the region-wide application could be related to many unaccounted factors, including variability in sampling dates, local microclimates, food sources, and levels of endemism. In addition, site-level variability could have created additional noise in our analysis. An advantage of using a presence-based indicator rather than proportional metrics based on relative abundances is that presence-based indicators can be incorporated into rapid assessment protocols because all organisms in the samples need not be counted and identified. Likewise, because of the high correlation between degree days and precipitation, the reliability of the indicator is nearly the same whether it is used to detect change in temperature or precipitation. The strongest effects (i.e., difference between groups detected by the indicator) appear to result from precipitation, which indicates that flow regime might be the dominant driver of variability in the benthic community.

The projection that climate change will result in regional temperature increases of 1 to 5°C in MCRs and the expectation that precipitation regimes will shift in a variety of ways among MCRs is well established (e.g., IPCC 2008, Cayan et al. 2009). Therefore, macroinvertebrate indicators like the one proposed here might be useful metrics for biological assessment programs that seek to monitor the effects of climate change. However, the effects of climate change might be more subtle than a single indicator alone can detect. This problem provides the incentive for obtaining additional information from measures based on selected biological traits.

Small streams in MCRs, particularly 1^{st}-order, nonperennial streams, might offer ideal conditions for monitoring climate change. Long-term studies are needed to develop effective indicators of climate change within specific ecoregions. Long-term monitoring and an understanding of species interactions are critical gaps in realistic predictions of the effects of climate change on benthic communities. Space-for-time substitutions are limited because of unaccounted site differences, which compound analytic difficulties. However, this approach is often the only available choice. Museum collections of benthic macroinvertebrates might provide a useful source of long-term information about changes in benthic macroinvertebrate communities (e.g., Resh and Unzicker 1975, Hall and Ide 1987, DeWalt et al. 2005). Life-history studies also are useful for making decisions about climate change. Without these studies, no alternative sources of information can be used. Unfortunately, the decline in these studies might limit the use of species-traits-based analyses (Resh and Rosenberg 2010), an approach that already has proven effective in European MCRs.

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