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 (MCRs) worldwide, including increases in temperature and decreases in rainfall in some areas, which could have important implications for biological assessment programs of aquatic ecosystems. We examined potential climate-change effects on aquatic communities using a consistently collected, 20-year benthic macroinvertebrate dataset from 4 sites along 2 small northern California streams. The sites represented unique combinations of stream order and flow intermittency. We found that the 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). Likewise, other common indices and metrics used in biological monitoring studies, such as the ratio of observed to expected taxa (O/E), percent 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 nine macroinvertebrate taxa, identified to genus level. This indicator was successful in detecting significant differences between years that were grouped based on temperature, precipitation, and a combination of temperature and precipitation. It was also successful in detecting significant differences between groups in an external dataset including 40 reference sites throughout the San Francisco Bay Area, which suggests that this indicator could be useful at larger spatial scales in this region. In addition, we found that two biological trait categories found in large, long-lived organisms decreased with increasing temperature and decreasing precipitation at the most intermittent site, indicating that climate change may selectively affect taxa with certain traits. The robustness of the B-IBI for northern California and other common indices and metrics to temperature and precipitation variability demonstrates their continued applicability for examining water quality under future climate change scenarios. However, it also suggests that they likely will not be good indicators for detecting climate-change effects. The impacts of climate change in Mediterranean-climate streams can be effectively monitored 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.

INTRODUCTION

Long-term studies in freshwater ecology are still relatively rare, particularly studies that span >10 years (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 within aquatic systems. Studies that span longer than 10 years 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

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have also established links between changes in macroinvertebrate communities and extreme climatic events (e.g., drought: Mouthon and Daufresne 2006, Bêche *et al*. 2009; freezing: Mulholland *et al*. 2009) and climatic cycles (NAO: Bradley and Ormerod 2001; and ENSO: Bêche and Resh 2007b, Gilbert *et al*. 2008), both of which may 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 and/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 documented shifts in community composition and structure are largely a result of selection towards temperature-tolerant and/or low-flow tolerant species (e.g., Chessman 2009). Research examining the effects of climate change on species traits has focused primarily on individual taxonomic groups rather than entire communities (e.g., Mouthon and Daufresne 2006, Cordellier and Pfenninger 2008, Spooner and Vaughn 2008, Clausnitzer *et al*. 2009, Hering *et al*. 2009). However, there is evidence that aquatic communities may experience dramatic shifts toward smaller size distributions with climate change, which 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 localized impacts (e.g., urbanization and agriculture), because the metrics for references sites (e.g., biotic indices) may be affected by climate change. 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). To date, the large majority of climate change research has been focused on temperate ecosystems, particularly in Europe (Rosenzweig *et al*. 2008), and aquatic macroinvertebrate research is no exception to this pattern. In particular, there has been little research in MCRs on potential climate-change impacts in aquatic ecosystems. Bêche and Resh (2007a,b) and Bonada *et al*. (2007) have conducted studies suggesting that climate change in MCRs may result in greater changes in taxonomic composition compared to changes in the biological traits (e.g., life history traits and size) in MCRs. However, there are few studies that explicitly examine the effects of climate change (e.g., temperature increase) on benthic macroinvertebrates in these climatic regions.

In the MCR of California, temperature and precipitation extremes over the past 20 year have been analyzed using a range of time-series analyses and 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 the end of this century (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 an extension of rainy season length with individual rainfall events occurring more sporadically (Cayan *et al*. 2009). In addition, most GCMs indicate that California will retain its characteristic Mediterranean climate with relatively cool and wet winters, and hot and dry summers.

Benthic macroinvertebrates are sensitive to changes in temperature, precipitation, and the associated flow regimes (e.g., 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), will likely impact benthic macroinvertebrates in MCR streams because temperature affects growth and timing of development and emergence (Bayoh and Lindsay 2003). Seasonal differences (i.e., rainy season vs. dry season) in the abundance and composition of benthic macroinvertebrates in the MCR of California are diminished during drought years and were correlated with patterns in the El Niño Southern Oscillation (ENSO), which are linked to temperature and precipitation (Bêche and Resh 2007b, Mazor *et al*. 2009). Although there is no evidence for an increase in the frequency or intensity of ENSO because of climate change, 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., taxa richness and EPT richness) are highly variable among years in coastal California streams, whereas other indices (e.g., B-IBI and 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.

The objectives of this study are to determine: 1) whether the core, multimetric indicator of biological assessment programs in northern California (i.e., the 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., percent EPT individuals, O/E scores); 3) whether taxa-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 land-use effects using biological monitoring programs in California because these programs are based on references conditions, which may be affected by climate change. If this is the case, multimetric indicators may have to be adjusted, e.g., by removing metrics sensitive to climate change to reliably detect disturbances associated with land-use. These implications of climate change may also be relevant to biological assessment programs in other MCRs worldwide, which include areas in parts of Europe, southern California, South Africa, Australia, and Chile (Gasith and Resh 1999).

METHODS

Study Site and Existing Data

This study is based on a 20-year, consistently collected benthic macroinvertebrate dataset. Studies based on datasets of comparable duration have made important contributions to understanding of climate change effects (e.g., Perry *et al*. 2005, Both *et al*. 2006, Rosenzweig *et al*. 2008). This dataset may be particularly valuable because it is of comparable length to most existing biological monitoring programs in the United States (e.g., Resh and Rosenberg 1989, Jackson and Füreder 2006) and thus the findings may apply directly to these programs. This dataset is also one of the most consistent datasets collected in that benthic macroinvertebrates were sampled each year by the same individual (V.H. Resh) and identifications were done by the same individual (E.P. McElravy). Each collection consisted of 5 Surber samples (0.093 m^2, 500-µm mesh), and all individuals within each sample were identified to genus or, when possible, to species (see Bêche *et al*. 2006 for additional detail).

The dataset is composed of collections from four sites along two small, 1st and 2nd order, northern California streams, Knoxville and Hunting Creeks, in Lake County and Napa County, California (Figure 1). The watersheds are relatively unaltered and are considered to represent reference conditions; see Bêche and Resh (2007a,b) and Mazor *et al*. (2009) for further details about these sites. There is evidence that the benthic macroinvertebrate communi-

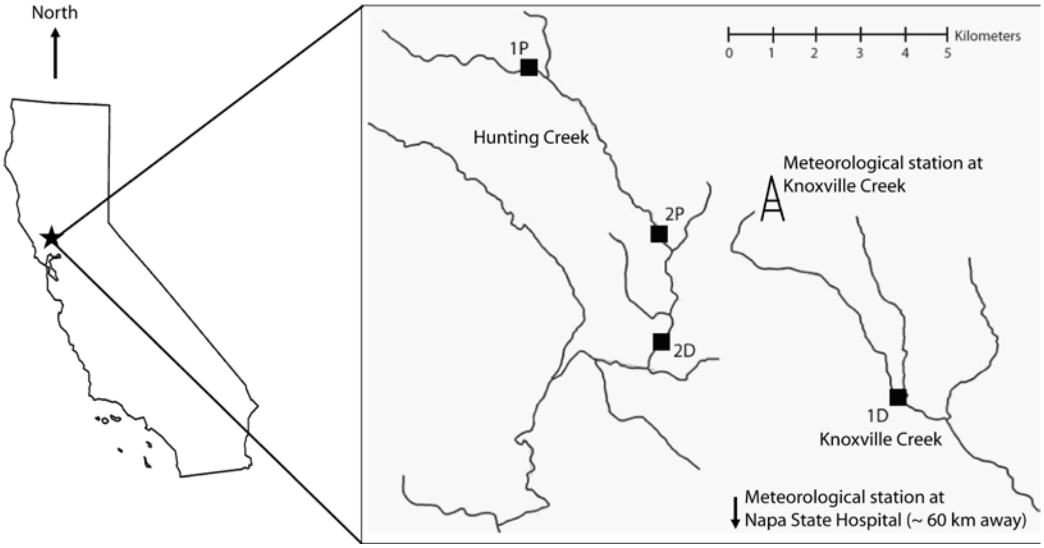

Figure 1. Site map showing streams as black lines. Site 1D is on Knoxville Creek and sites 1P, 2P, and 2D are on Huntington Creek.

ties 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 conducted annually near April 15 from 1984 to 2003 at three of the sites (sites 1D, 2D, 2P), and from 1985 to 2003 at one of the sites (site 1P). Samples were collected in a random design, stratified within riffles, with the same riffles sampled each year. Two of the sampling sites are characterized by non-perennial flow (1D, 2D) and two are characterized by perennial flow (1P, 2P). Watershed areas range from 2 to 29 km2, and the sites are all within a 500-m elevation range (Table 1). The sampling date represents the end of the wet season, when the majority of pre-emergence growth in all benthic macroinvertebrate orders occurs in this region (Mendez and Resh 2008).

Temperature and Precipitation

Daily air temperature records were obtained from the meteorological station located near Knoxville Creek within the University of California McLaughlin Nature Reserve (Figure 1). These daily air temperature records covered the entire duration of the study except for the first year and some short gaps over the remaining years (<23 days). To create a complete, daily dataset for the study duration, the daily air temperatures at Knoxville Creek were plotted against those at Napa State Hospital, which is approximately 60 km south of the study sites, and any missing values were filled in using the equation determined from a linear regression between the data from these two stations.

Daily air temperature records were used to calculate degree-days, which have been shown in many studies to correlate with insect development (e.g., Wilson and Barnett 1983). To calculate degree-days, a threshold air temperature of 10˚C was used as a baseline because it is within the range of many macroinvertebrate species (e.g., Corkum 1992), and the number of days that exceeded this threshold was calculated over the 15-week period leading up to the sampling date, January 1 to April 15; the threshold temperature is the lower limit for invertebrate growth and development. We used a uniform value of the threshold temperature because we were seeking only to distinguish warm years from cold years from an invertebrate development perspective and not to elucidate distinct differences among the many aquatic species collected.

Daily precipitation records were obtained from the Napa State Hospital for the entire 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-week period leading up to the sampling date (i.e., January 1 to April 15) was calculated to create a precipitation variable for analysis. We limited the analysis to the calendar year rather than to the start of the wet season in California, which typically begins in October to early November, or to the water year, which begins October 1, in order to maintain consistency with the temperature analysis. 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 it is not crucial to start at the beginning. Furthermore, we observed that 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.

The relationship between air temperature (degree-days) 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.

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	8-Mar
2D	Hunting Creek	2	Nonperennial	22.1	38°49'45"	122°22'45"	402	15-Oct
1P	Hunting Creek	1	Perennial	4.4	38°51'56"	122°24'54"	634	10-May
2P	Hunting Creek	2	Perennial	29.3	38°48'30"	122°22'36"	348	15-Oct

The years were ranked by number of degree-days and by rainfall over the 15-week period leading up to the sampling date. These rankings were used to establish three groups: 1) cool vs. warm, 2) wet vs. dry, and 3) cool and wet vs. warm and dry for comparison, each comprising seven years. The cool/wet and warm/dry groups were established by multiplying the rankings for temperature and precipitation together to create a combined ranking that was used to sort years.

Although 20 years of the study period in this dataset were particularly dry compared to the past 50 years (Bêche *et al*. 2009), each year group was distinct (Table 2). For example, the average number of degree-days in cool years (28) was significantly different from warm years (53), 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 if there was substantial interannual variability during the study period, it would still be informative. In the very least, analyzing climate variability in the past would underestimate future climate changes, which are anticipated to be more extreme than those that have occurred in the past (IPCC 2008). The third grouping, i.e., the cool and wet vs. warm and dry, was developed to determine if a subtle, synergistic effect between temperature and precipitation may be evident in any of the metrics.

Macroinvertebrate Analyses

Collection Data

The data from the five benthic macroinvertebrate samples for each collection event were combined by taking the average to avoid pseudoreplication in comparisons among sites. This composite dataset was used to calculate a presence/absence matrix. Biological trait information was collected for nearly all of the taxa in the dataset 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, which was primarily a result of the aggregation of Chironomidae to family and the elimination of semi-aquatic Hemiptera. In addition, converting these taxa for O/E score calculation further reduced the number to 125 OTUs, just for the O/E analyses.

Independence among sites was examined using non-metric multidimensional scaling analysis (NMS) on the log10 (n + 1) taxa abundances of all taxa. The computer program PC-ORD 4.27 was used to obtain 2-D solution based on Sørenson distance (McCune and Mefford 1999). Clustering among the sites in ordination space was examined in relation to the categorical variables of stream order and perenniality. The NMS 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), which is used in California by state agencies to evaluate local anthropogenic stresses on stream communities (Rehn *et al*. 2007). The eight metrics that comprise the North Coast B-IBI include: EPT richness, Coleoptera richness, Diptera richness, percent intolerant individuals,

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

percent non-gastropod scraper individuals, percent predators, percent shredder taxa, and percent non-insect taxa. These metrics were calculated from the data collected using a Monte Carlo simulation without replacement to standardize sample size to 500 individuals, as required by the B-IBI (Rehn *et al*. 2005). For each site, the response of these metrics to both degree-days and total precipitation (for the 15-week period prior to sampling) was determined using linear regression. In addition, the average B-IBI value was examined between the *a priori* groupings (e.g., cool vs. warm, wet vs. dry, and cool/wet vs. warm/dry) using Student's *t*-tests This categorical comparison was used to determine if there was any evidence that the B-IBI could be used as an indicator of climate change for this locality.

Several additional widely used indices and metrics were evaluated to determine if they were responsive to temperature and precipitation change: percent EPT individuals, total richness, and EPT richness divided by the richness of Odonata, Coleoptera, and Hemiptera (EPT/OCH, Bonada *et al*. 2006). We also calculated the ratio of O/E(50) taxa from a RIVPACS-type model developed for California (see Ode *et al*. 2008 for details about this model). Each metric and index was plotted against degree-days and precipitation, and fit with linear regression. Using *t*-tests, values for cool years were compared to values for warm years, values for wet years to values for dry years, and values for cool and wet years to values for warm and dry years. A *p*-value of 0.2 was selected as a threshold of significance in order to reduce the probability of false negatives (Type II error) for marginally affected metrics; no metrics were strongly affected. Because this was primarily an exploratory analysis that was not intended to rigorously establish significance, Bonferonni corrections were not taken into account.

Local Climate Change Indicator

The final climate-change indicator was based on annual presence/absence data from the taxa observed at all four sites, thereby equally weighting effects on taxa that were less common in the dataset. To construct the final indicator, individual temperature (warm vs. cool) and precipitation (dry vs. wet) indicators, hereafter referred to as preliminary temperature and precipitation indicators, were developed from the dataset using an iterative process that used only a randomized subset of the data. For example, the 1st iteration of the preliminary temperature indicator used six of the seven years that fit the warm and cool criteria, respectively. Within the warm group, 6 years of data at 4 sites yielded a total of 24 sampling events for screening. The one year that was randomly withheld from the seven years 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 group compared to the cool group by at least 8 out 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 within this iteration. The total number of taxa selected by this process was calculated for each iteration. In the 1st iteration, for example, 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. Therefore, we calculated 24 different proportions per iteration from these 6 years of data (4 sites per year) and calculated the mean and standard error of this proportion. A *t*-test was then performed comparing the preliminary temperature indicator between warm years (8.2/12) and cool (3.3/12) years, in our 1st iteration example.

The internal validation was completed simultaneously with the taxa screening process. For example, in the 1st iteration mentioned above 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 year of data that was withheld for internal validation, which was recorded as the proportion present out of those 12. Therefore, we calculated four different proportions per iteration from this one year of data. A *t*-test was then performed comparing the preliminary temperature indicator between warm years (7.3/12) and cool years (7.8/12). When the result was significant, the taxa of 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 six years 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, we set a criteria for taxa that resulted in significant *t*-tests between groups in the internal validation on at least 4 occasions out of 20 possible comparisons (e.g., the taxa had at least 4 points). For example, the caddisfly genus Hydroptilia, which was included in the final indicator, was involved in five out of the five significant temperature models and two out of the five significant precipitation models, and was therefore significant on seven total occasions. The goal behind 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. Lastly, 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 then performed 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 using a dataset 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 dataset were collected using a targeted-riffle sampling method (Barbour *et al*. 1999). The majority of sites were sampled by the San Francisco Regional Water Quality Control Board through the Surface Water Ambient Monitoring Program (SWAMP). Additional sites were sampled by 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 dataset, the two wettest years (2005, 2006) and two driest years (2001, 2007) were selected from this eight-year period. The average value of the climate change indicator and the standard error of this value were calculated for each of these 2 precipitation groups (wet and dry) using the final taxa that were selected for the indicator from the 20-year study dataset. These values were compared with each other (i.e., wet years and dry years) using a *t*-test. If the values were significantly different, the external validation was deemed successful.

Lastly, the value of the final climate change indicator was calculated for the original groups containing seven years of data for each site (i.e., cool vs. warm, wet vs. dry, and cool and wet vs. warm and dry). The average value and the standard error were calculated for each group. The differences between groups were evaluated using a *t*-test.

Biological Traits

Three biological traits (voltinism, maximum body size, and desiccation resistance) were examined, which 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 would likely show a response to climate change effects.

The distribution of biological traits among taxa was calculated using the presence-absence matrix instead of 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. Because the fuzzy coding approach was used (Chevenet *et al*. 1994), each taxon could be described by a fractional composition of multiple trait categories, e.g., a taxon could be described as 0.4 semivoltine and 0.6 bivoltine, with the fractions summing to 1, which would indicate that this taxon has partial semivoltine and partial bivoltine characteristics.

RESULTS

Physical Conditions

The daily average air temperatures measured at Knoxville Creek had a linear relationship ($R^2 = 0.78$) with those measured at Napa State Hospital ($y = 1.3x - 4.5$). Therefore, we assumed that air temperatures, and thus the degree-days that were calculated for the sites, were comparable at each site. The degree-days and precipitation from January 1 to April 15 were highly variable from year to year. Degree-days ranged from a minimum of 44 in 1998 to a maximum of 243 in 1985, a 5-fold difference. Precipitation ranged from 14 cm in 1984 to 70 cm in 1986, a 5-fold difference. This high inter-annual variability is evident among the temperature and precipitation values characterizing the different year groupings (Table 2).

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

The NMS plot revealed distinct clusters of non-perennial and perennial sites, and of 1st- and 2nd-order sites (Figure 3), indicating that the benthic macroinvertebrate communities at each site could be treated independently to some extent, despite being within the same watershed. The 1st axis on the NMS 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 (Figure 3).

Biological Metrics

The North Coast B-IBI did not change significantly with temperature and precipitation at any site (Figure 4); however, the power was low (i.e., <0.8 in each case), which reflects a limited ability to detect a difference. Furthermore, there were no significant differences in the B-IBI between cool and warm or wet and dry years (Table 3). The only significant ($p \leq 0.05$) regressions among the eight component metrics of the B-IBI were Coleoptera rich-

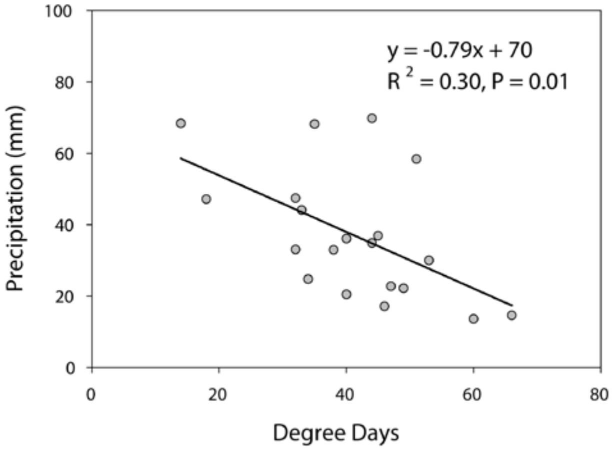

Figure 2. Linear regression of total precipitation against degree-days, both calculated from the 15 weeks (January 1 to April 15) leading up to the sampling date.

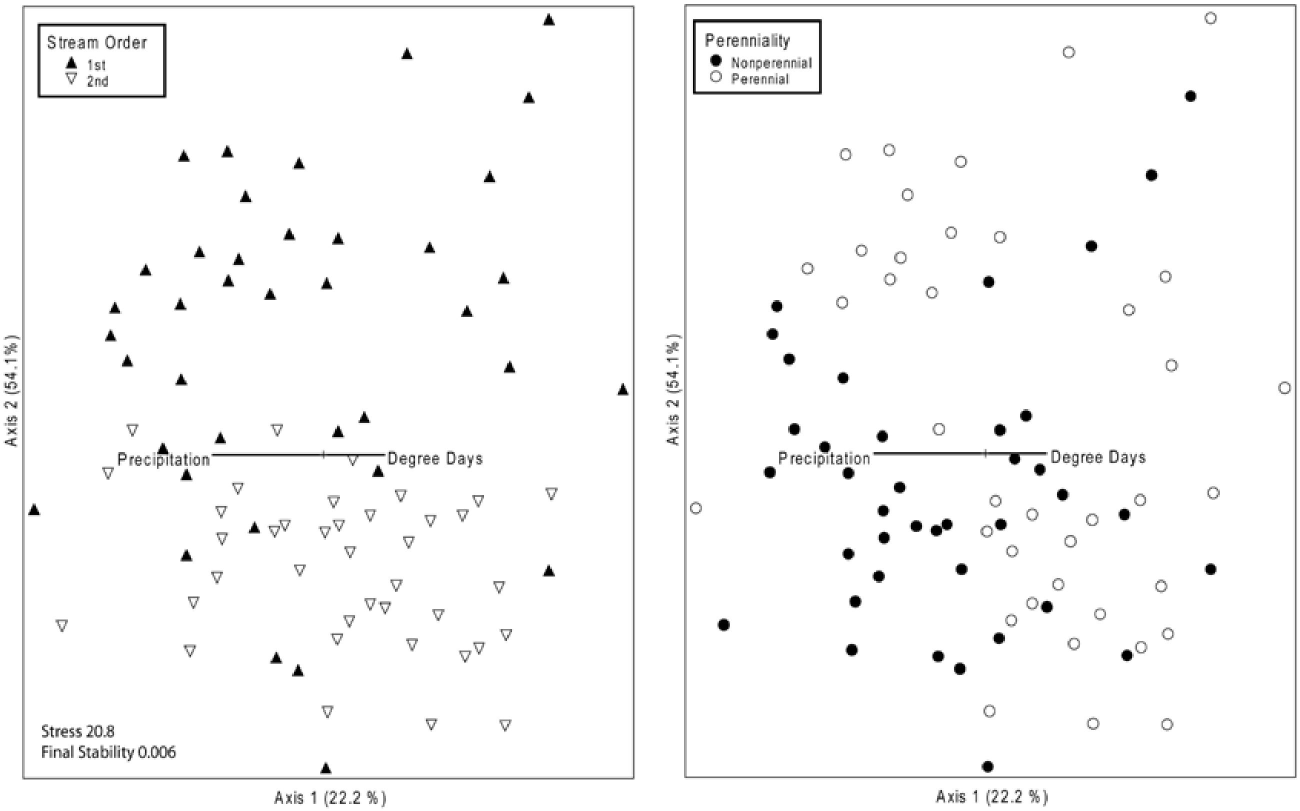

Figure 3. Clustering of taxa using 2-D non-metric multidimensional scaling analysis with axis 1 aligned with degree-days.

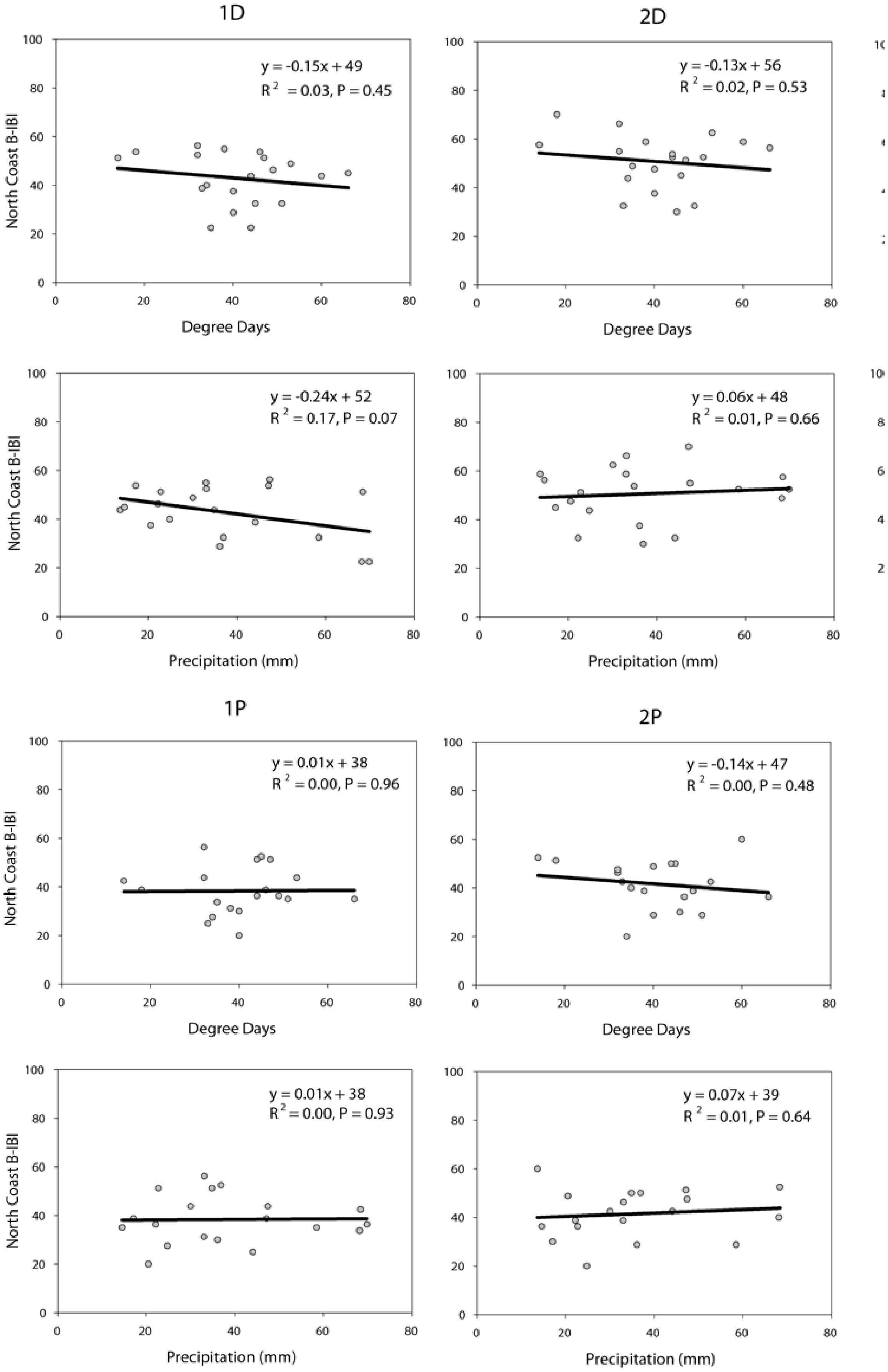

Figure 4. The North Coast B-IBI plotted against degree-days and precipitation and fit with linear regression trend lines.

ness against degree-days at site 1P (Table 4) and percent shredder taxa against precipitation at site 1D (Table 5). In the regressions of metrics against degree-days, Coleoptera richness, percent intolerant individuals, percent non-gastropoda scraper individuals, and percent non-insect taxa had regressions with *p*-values ≤0.2. In the regressions of metrics against precipitation, EPT richness, Coleoptera richness, percent intolerant individuals, percent predators, and percent shredder taxa had regressions with $p \leq 0.2$. Coleoptera richness and percent intolerant individuals were correlated with both degree-days and precipitation, suggesting that these two metrics may be the most responsive to climate change. However, Coleoptera richness showed different directional responses in sites 1D and 2P.

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

Local Climate Change Indicator

The differences in taxa occurrence between groups (i.e., warm vs. cold and wet vs. dry) ranged from 0 to 15 in most of the iterations and were close to 0 for most of the 206 total taxa; a difference of at least 8 was the criteria 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 (i.e., cool vs. warm and wet vs. dry) in all of the groups containing the 6 years of data from which the indicators were constructed. In these same 20 iterations, the preliminary indicators detected a significant difference between groups in half of both the cool vs. warm groups (iterations 1, 2, 5, 6, and 10) and wet vs. dry groups (iterations 1, 3, 6, 7, and 9) that contained the 1 year of data that was withheld for internal validation purposes. Thus, the internal validation indicated that this method adequately selects taxa 50% of the time.

Of the 13 total genera that were 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 at least 4 out of 20 of the iterations in the internal

Table 3. Comparison of average metric and index values between cool and warm years, wet and dry years, and cool/wet and warm/dry years; asterisks are used to denote comparisons considered to be affected by climate change (p ≤ 0.20).

Metric	Site	Cool Years	Warm Years	*p* -value	Wet Years	Dry Years	*p* -value	Cool/Wet Years	Warm/Dry Years	*p* -value
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 (0.460)	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 (0.010)	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
Percent 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)	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 (13.0)	21 (7.7)	0.80
	2P	39 (11.0)	51 (9.5)	0.42	34 (8.8)	47 (8.3)	0.28	38 (15.0)	45 (10.0)	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 (0.8)	22 (2.4)	0.18*	4 (1.3)	2 (0.2)	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	4.0 (0.97)	2.6 (0.6)	0.26	4.2 (1.0)	2.1 (0.12)	0.05*
	2D	4.37 (0.53)	4.21 (1.16)	0.90	2.4 (0.23)	3.2 (0.4)	0.09*	2.7 (0.3)	2.8 (0.19)	0.80
	1P	2.87 (0.48)	1.53 (0.25)	0.03*	2.7 (0.35)	1.8 (0.4)	0.13*	2.8 (0.4)	1.6 (0.47)	0.09*
	2P	2.90 (0.19)	2.53 (0.23)	0.23	23.0 (0.98)	19.0 (2.6)	0.15*	3.5 (1.2)	2.8 (0.22)	0.55

Table 4. Linear regression parameters of the component metrics of the North Coast B-IBI plotted against degree days; trends with increasing temperature are marked with asterisks for relationships considered to be affected by climate change (p ≤0.20).

Regression Variable	Site 1D			Site 2D			Site 1P			Site 2P		
	R^2	*p* -value	Trend	R^2	*p* -value	Trend	R^2	*p* -value	Trend	R^2	*p* -value	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		0.02	0.51	
% Non-Gastropoda Scraper Individuals	0.00	0.90		0.01	0.68		0.10	0.18	Increase	0.02	0.51	
% Predators	0.09	0.70		0.02	0.56		0.01	0.71		0.03	0.46	
% Shredder Taxa	0.07	0.26		0.06	0.29		0.16	0.09	Decrease	0.02	0.53	
% Non-Insect Taxa	0.01	0.74		0.10	0.18	Decrease	0.02	0.56		0.00	0.78	

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 contained within 3 orders; Trichoptera (n = 4), Diptera (n = 3), and Hemiptera (n = 2). Because trichopterans made up 23% of the overall taxa list and 44% of the taxa in the indicator (i.e., 4 of the 9 taxa selected), 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).

Table 5. Linear regression parameters of the component metrics of the North Coast B-IBI plotted against precipitation; trends with increasing precipitation are marked with asterisks for relationships considered to be marginally affected by climate change (p ≤0.20).

Regression Variable	Site 1D			Site 2D			Site 1P			Site 2P		
	R^2	*p* -value	Trend	R^2	*p* -value	Trend	R^2	*p* -value	Trend	R^2	*p* -value	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		0.06	0.30	
Diptera Richness	0.00	0.82		0.05	0.37		0.01	0.68		0.02	0.57	
% Intolerant Individuals	0.08	0.23		0.01	0.71		0.14	0.12*	Increase	0.01	0.71	
% Non-Gastropoda 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	
% Non-Insect 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 at least 1 of the internal validation iterations that detected a significant difference between groups (i.e., cool vs. warm and wet vs. dry). The taxa included in the final indicator are marked with an asterisk and were selected based on having at least three points, which are the occurrence sums across the rows.

Taxa	Cool Years vs. Warm Years Iteration					Dry Years vs. Wet Years Iteration					Occurrences (Points)
	1	2	5	6	10	1	3	6	7	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

The final climate change indicator was able to detect a significant difference between the groups (i.e., warm vs. cool, wet vs. dry, and cool and wet vs. warm and dry) in 10 out of the 12 comparisons examined (Table 8). The difference in the average indicator value for all the sites combined was highest between the dry years and wet years (6.8 - 2.7 = 4.1); the difference between the cool and warm years and the wet and dry years was 2.8 in each case. This agrees with the NMS plot (Figure 3) that was performed on the raw abundance data for all the taxa, which shows that precipitation is 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 non-perennial sites than in the perennial sites.

The indicator developed from the 4 study sites in two streams with long-term data was robust when compared with the external validation at 47 sampling events at 40 sites from throughout the greater San Francisco Bay Area. A difference in the indicator value of 0.8 units was observed between wet years in the regional dataset, which had an indicator value of 1.9, and dry years, which had an indicator value of 2.8. Although this difference was smaller than that observed in the local dataset (i.e., 2.8), it was still statistically significant ($p = 0.001$). All but one of the nine taxa were prevalent in both the local and regional dataset, with the exception being *Ambrysus*.

Biological Traits

Consistent trends between cool and warm years, and wet and dry years, were detected in two of the three selected traits. However, these trends were only statistically significant at the site with the most extreme conditions of intermittency, i.e., the 1st order, non-perennial (1D) site (Figure 5). The trends included a decrease in macroinvertebrates with a life-cycle lasting longer than 1 year, and a decrease

Table 7. Number of times (out of 28 sampling events) that presence of the component taxa was documented for the final climate change indicator, observed during cool and wet years (7 years total), and warm and dry years (7 years total).

Genus (Order)	Number of Times Present in Cool/Wet Years	Number of Times Present in Warm/Dry Years	Absolute Difference Cool/Wet vs. Warm/Dry Years
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

in those with a body size of >40 mm with increasing temperature or with decreasing precipitation. Desiccation resistance, which was also hypothesized to be potentially responsive to temperature, did not show consistent or significant responses among sites (Figure 5).

Cool and Wet versus Warm and Dry Years

The subset of cool and wet years, and warm and dry years, which represents the strongest combination of climate change effects examined, did not have a notably stronger influence on most of the metrics and indices. However, the difference in total richness between cool and wet years, and warm and dry years, was statistically significant at one of the sites (2P), whereas it was not significant for any of the individual temperature or precipitation comparisons (Table 3).

DISCUSSION

The high inter-annual variability in temperature and precipitation that was observed among years in this 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 non-linearly associated with winter precipitation anomalies (Pozo-Vázquez *et al*. 2005). In contrast, in the MCR of Southern California, there has been a tendency towards higher than normal precipitation during El Niño winters (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 variability in MCRs over the past millennium (Mann 2006).

The significant inverse correlation between temperature and precipitation illustrates that the effects observed in this study could relate 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 may not be direct. For example, water temperature is inversely correlated with dissolved oxygen levels in streams and rivers, which can affect benthic macroinvertebrates (e.g., Morrill *et al*. 2005, Jacobsen and Marín 2007). In addition, the mechanism of the effect of dissolved oxygen on benthic macroinvertebrates could relate to other unmeasured explanatory variables such as amount of canopy cover or groundwater input. These mechanisms

Table 8. Average value of the local climate change indicator in the different year groups with standard error in parentheses; significant comparisons are marked with asterisks.

Site	Cool Years	Warm Years	*p* -value	Wet Years	Dry Years	*p* -value	Cool/Wet Years	Warm/Dry Years	*p* -value
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)	0.1	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	

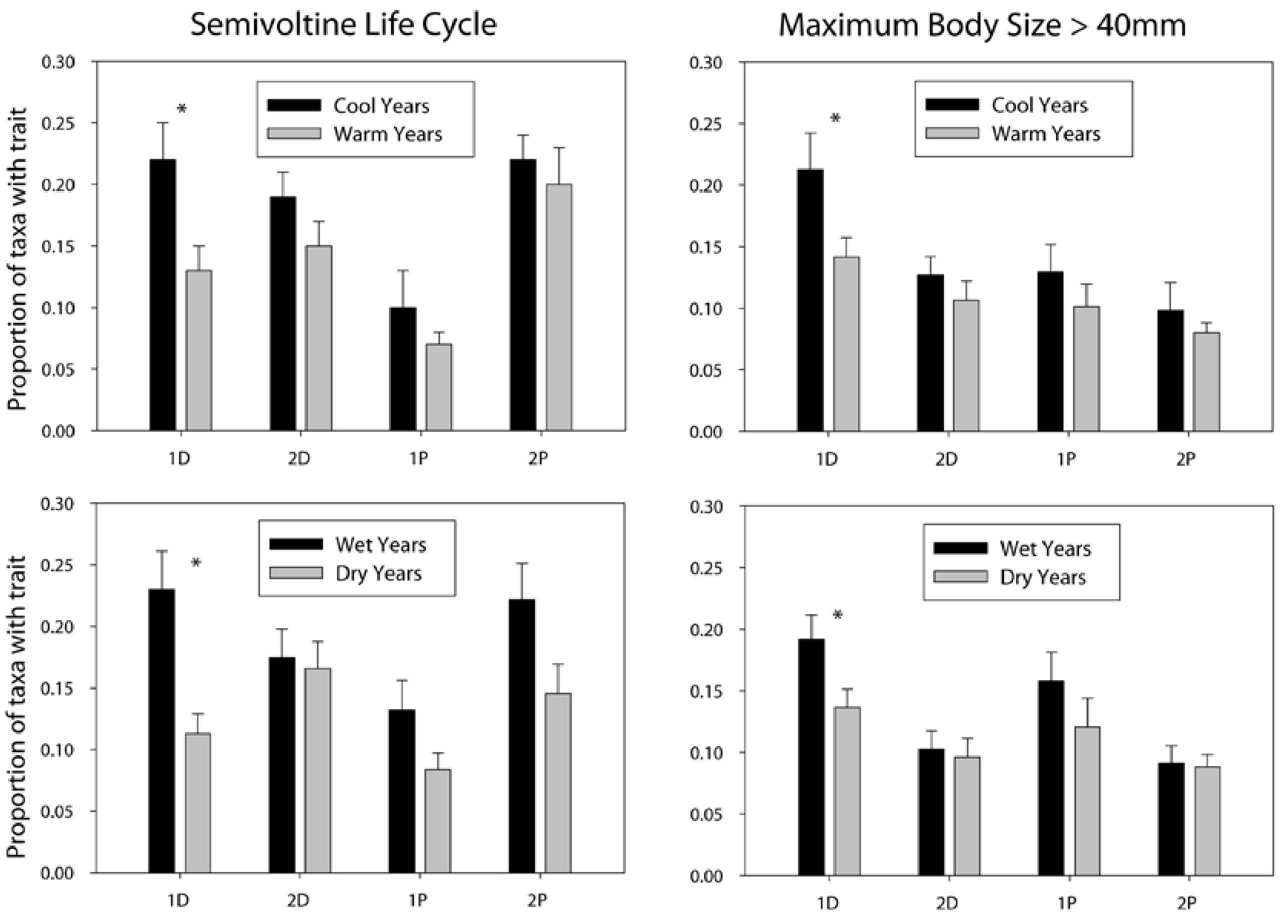

Figure 5. Comparison of biological trait presence at the study sites between cool and warm years (±SE); an asterisk denotes a significant difference ($\alpha = 0.05$) between cool and warm years that was determined using a Student's *t*-test.

could not be tested directly because year-to-year variability of these variables was not collected.

The benthic macroinvertebrate communities observed in the perennial and non-perennial and in the 1st and 2nd order sites were distinct, which is in agreement with the findings in Bêche and Resh (2007a,b), and Bêche *et al*. (2009), and Mazor *et al*. (2009). Similarly, the importance of perenniality and stream order in shaping distinct benthic communities has been documented in studies conducted in the MCRs of Europe (e.g., Bonada *et al*. 2007, Anna *et al*. 2009) and of 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 this study was that the 1st order, non-perennial combination at site 1D shows the greatest association between biological traits and climate, probably because it represents the most extreme, intermittent conditions. The longer-lived (life cycle >1 year), larger organisms (maximum body size >40 mm) at this site were clearly less abundant in warmer and in drier years, which relates to their lower tolerance to extreme conditions.

Because some of the most widely used biological metrics (e.g., percent EPT, total richness) and local indices (e.g., the North Coast B-IBI) were robust against inter-annual temperature change and precipitation change, these metrics should have continued usefulness for biological assessment programs aimed at detecting local anthropogenic stressors under climate change scenarios. However, the low power (<0.8) indicates that these findings should be interpreted cautiously. A fairly constant percent composition of the same dominant taxa was observed among the years, which indicates that the foundation of the benthic community may remain intact despite temperature and precipitation changes. This apparent resilience may relate 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 ratio because of the higher EPT composition. However, an unpolluted site can have low EPT/OCH if the riffles are relatively less common than pools in the system (Bonada *et al*. 2006). The EPT/OCH ratio was lower in the warm than in the cold years at all the sites, and lower in the dry than in the wet years in three out of the four sites, although not all of these differences were statistically significant. A combination of polluted water and increasing temperature may have a compounded, negative impact on metrics that are based on the OCH orders, and this possibility should be tested further.

The B-IBI for northern California along with other commonly used metrics and indices may be unresponsive to the expected scenarios of climate change because many of the component metrics are at the order level; genera may come and go, but with replacement, resulting in the order metrics being unchanged. However, we found that 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 may result from its ability to account for generic-level turnover, because it is based on individual taxa. These taxa, which were dominated primarily by trichopterans, may be among the most susceptible to climate change and could be a useful component to include in biological monitoring programs aimed at detecting climate-change effects.

The debate about the general usefulness of higher levels (e.g., order and family) compared to lower levels (e.g., genus and species) of taxonomic resolution for evaluating anthropogenic changes has gone on for decades (e.g. Resh and Unzicker 1975). Lenat and Resh (2000) provide many examples of when species or generic-levels may be more useful than higher levels. The potential usefulness of generic-level indicators for detecting climate change, which was a key finding of this study, suggests that this result should be added to that list as well.

There was modest evidence for a filtering effect on biological traits in the site with the most extreme conditions of intermittency, which indicates that the benthic communities that exist in intermittent habitats may experience the strongest selective force under the expected conditions of climate change. This 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 macroinvertebrates in North American freshwater studies. Although 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, any evolutionary response that would occur would be 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 may depend on the extremeness or severity of changes at a site, which tend to be highest in 1st order, non-perennial streams. The severity of changes 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 that we used in this study. Such an indicator might also be applicable at a regional-scale, as evidenced by the successful external validation using sites throughout the San Francisco Bay Area. It is important to note, however, that the strength of the signal was lower between groups in the regional dataset. The reduced signal strength in the region-wide application could relate to many factors that were not accounted for, including variability in sampling dates, local microclimates, food sources, and levels of endemism. Additionally, most of the sites were unique in the dataset and it is possible that site-level variability led to additional noise in this analysis. An advantage of using a presence-based indicator as opposed to proportional metrics based on relative abundances is that it can be incorporated into rapid assessment protocols because all of the organisms in the samples do not need to 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 detecting change in temperature or precipitation. The strongest effects (i.e., the difference between the groups as detected by the indicator) appear to result from precipitation, which indicates that the flow regime of the sites may 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, such as the one proposed in this study, may be a useful metric for biological assessment programs that seek to monitor the effects of climate change. However, the effects of climate change may be more subtle than a single indicator alone can detect, which provides the incentive for obtaining additional information from measures based on select biological traits.

Small streams in MCRs, such as those included in this study, may provide ideal conditions for monitoring climate change, particularly 1st order, non-perennial streams. Similar long-term studies are needed to develop effective indicators of climate change within specific ecoregions. Long-term monitoring and an understanding of species interactions with each other are critical gaps in realistic predictions of the effects of climate change on benthic communities. Space-for-time substitutions have limitations in terms of unaccounted site differences, which compound analytic difficulties. However, this approach is often the only available choice. Museum collections of benthic macroinvertebrates may 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 are also useful for decision-making about climate change and; without these studies, there are no alternative sources of information that can be used. Unfortunately, the decline in these studies may 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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