

DRAMATIC DECLINES IN MUSSEL BED COMMUNITY DIVERSITY: RESPONSE TO CLIMATE CHANGE?

JAYSON R. SMITH,^{1,3} PEGGY FONG,¹ AND RICHARD F. AMBROSE²

¹Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive, South, Los Angeles, California 90095-1606 USA

²Environmental Science and Engineering Program, Department of Environmental Health Sciences, University of California Los Angeles, Box 951772, Los Angeles, California 90095-1772 USA

Abstract. Mussel beds along the wave-exposed coast of the eastern North Pacific Ocean serve as an important habitat, harboring a high diversity of species. A comparison of California mussel bed community diversity in 2002 to historical data (1960s to 1970s) revealed large declines (mean loss 58.9%), including some declines >141 species (~80% loss). Concurrent work revealed inconsistent changes in mussel populations (biomass and bed thickness) along the California coast, suggesting that diversity declines may be related to large-scale processes rather than local habitat destruction. Potential factors causing declines in mussel community diversity are discussed, with regional climate change associated with the Pacific Decadal Oscillation and climate change-induced alterations of ecological interactions and biological processes suggested as likely causes. Although extensive literature has predicted the potential effects of climate change on global diversity, this study is one of the few examples of declines attributed to climate change.

Key words: biodiversity; biological diversity crisis; climate change; historical change; *Mytilus californianus*; mussel bed diversity; Pacific Decadal Oscillation; rocky intertidal.

INTRODUCTION

Biodiversity is an integral part of ecosystem function (Bengtsson et al. 1997, Grime 1997, Loreau et al. 2001), affecting ecosystem productivity, decomposition rates, nutrient cycling, stability, and resistance to perturbations (Schulze and Mooney 1993, Naeem et al. 1994, Tilman et al. 1996, Loreau et al. 2001, Tilman et al. 2001). Declines in biodiversity are of great concern as forces such as habitat destruction, global environment change, pollution, and exotic species cause continued extinctions and declines in species abundances and community biodiversity (Pimm et al. 1995, Sala et al. 2000). The rate of diversity loss has been estimated to be about 400 times that recorded through geological history (Wilson 1985), with projected extinction rates resulting in loss of half of the existing number of species if current patterns of global change continue (Smith et al. 1993). An integral part of understanding the crisis of biodiversity loss is continued investigations and documentation of long-term community change.

In exposed rocky intertidal habitats of the northeast Pacific Ocean, mussels (mostly *Mytilus californianus* Conrad) dominate the midintertidal zone (Ricketts et al. 1968), aggregating into large beds that provide a

microhabitat for a diverse assemblage of species (Suchanek 1992). Beds are composed of a structurally complex matrix of living mussels, shells, sediment, and debris that provides food and shelter for up to 300 associated species at a given location (Suchanek 1979) and 750 species in a region (Kanter 1980). This microhabitat is considered one of the world's most diverse temperate systems (Suchanek 1992). Multilayered mussel beds protect associated species from harsh environmental conditions, with lower light, temperature, and wave force, and higher sedimentation and humidity below the surface (Suchanek 1979). The mussel matrix also provides a refuge from predation for some species as well as a large amount of available surface area for the settlement of sessile species (Suchanek 1979).

The purpose of this study was to resample mussel bed-associated species diversity at sites studied in the late 1960s and 1970s to investigate changes in species richness and diversity over time.

METHODS

In 2002, mussel (*Mytilus californianus*) bed communities at 22 sites previously studied in the 1960s and 1970s were resampled using identical sampling methods and identical plot size for comparison with historical data. Extensive data from the late 1960s and 1970s documented high diversity of fauna in mussel beds (Cimberg 1975, Straughan and Kanter 1977, Kanter 1977, 1978, 1979, Straughan 1978) along a large geographic region (~1300 km) on the California coast. Five randomly located 0.03-m² plots were harvested within the middle

Manuscript received 1 August 2005; revised 9 November 2005; accepted 17 November 2005. Corresponding Editor: S. G. Morgan.

³Present address: Department of Biological Science, California State University, Fullerton, P.O. Box 6850, Fullerton, California 92834-6850 USA.
E-mail: jasmith@fullerton.edu

of established mussel beds, and all flora, fauna, sediment, and debris from each core was collected and fixed in 10% formalin seawater. For each harvested core, we quantified density and diversity of associated invertebrate macrofauna, identifying all individuals to species or the lowest identifiable taxonomic level. As was done with historical data, total invertebrate species richness was quantified for pooled cores, encompassing a total area of 0.15 m² (5 × 0.03 m²) with a few exceptions: 18 of 22 sites used five 0.03-m² cores, while three 0.02-m² plots were used at Trinidad (Cimberg 1975) and six to nine 0.05-m² cores were used at Cayucos, Morro Bay, and Montana de Oro (Kanter 1977). To facilitate an identical number of harvested plots for comparisons, two of the five 0.03-m² plots harvested in 2002 at Trinidad were randomly chosen, and five of the cores reported at Cayucos, Morro Bay, and Montana de Oro in 1977 were randomly chosen for each site. To facilitate further comparisons of diversity with historical studies, Pielou's evenness was calculated for all 22 sites using pooled invertebrate counts from the total number of cores at each site. Pielou's evenness is an index of species diversity that not only measures the number of species but also the evenness or equitability of the abundances of those species.

We considered several potential methodological sources of error, including seasonal change in diversity and difference in tidal heights of sampling positions. However, these were not a likely source of error, as seasonal and tidal height differences in species richness were investigated in the past and shown to be variable but not a significant factor (Straughan and Kanter 1977, Straughan 1978, Kanter 1979). For example, Kanter (1979) sampled five sites in southern California during a series of different seasons and found that diversity during the different periods varied little, often by less than five species. Furthermore, Kanter (1979) sampled mussel community diversity at two tidal heights at four sites in southern California (range in tidal height difference, 0.03–2.41 m) and found that diversity difference ranged from one to seven species equally in either direction. In addition, we feel these potential errors are not significant, as our data were compared with data from similar seasons when possible and from harvested cores taken from the middle of mussel beds, as was done in the past.

Species richness and Pielou's evenness were compared between historical data and 2002 data using a pairwise *t* test. Analyses were conducted on all sites as well as within geographic regions. Sites were classified into three geographic regions: southern California mainland region, southern California island region, and central/northern California region. Within the central/northern California region, four of the five sampled sites occurred along the southern portion of central California, while the remaining site was ~700 km north in Humboldt County.

RESULTS

The total richness of invertebrates collected within mussel beds in 2002 was dramatically lower than earlier collections at all 22 sites sampled along the coast of California (Fig. 1), with the losses ranging from 24% (10 species) to 81% (141 species) and a mean loss of $58.9 \pm 3.8\%$ (mean \pm SE; 60.2 species). Although diversity varied substantially in past studies (42–174 species), current richness was much lower with a narrower range (20–51 species). Mean richness found in the past at all 22 sites was 94.5 ± 7.4 , while the current mean was significantly lower at 34.3 ± 1.7 (pairwise *t* test on log-transformed data; $t = 10.7$, $df = 21$, $P < 0.0001$). Richness declined within all geographic regions (pairwise *t* test, southern California mainland $t = 7.2$, $df = 6$, $P < 0.0001$; southern California Channel Islands $t = 6.7$, $df = 9$, $P < 0.0001$; central/northern California $t = 3.5$, $df = 4$, $P < 0.02$), even in central/northern California where richness was found to be lower than other regions in the past (Fig. 1). However, the pattern of diversity declines encompassing the entire California coast is provisional due to only one of the five sites in the central/northern California region being located north of Monterey Bay.

Species were grouped into a higher taxonomic level in order to determine if certain taxa recorded greater species diversity losses than others. At sites where species lists were included in historical studies, we were able to compare the macroinvertebrate groups with those in 2002. We found that a majority of the higher taxa declined between 40% and 60%. The only exceptions occurred in the Cirripedia and Decapoda arthropods and the echinoderms, whose richness remained the same over time, although these were not very diverse groups during either sampling period.

Contrary to trends observed in species richness, Pielou's evenness did not consistently show declines; although highly variable, there were relative increases in evenness at five sites and no change at eight sites (Fig. 2). In addition, comparing Pielou's evenness in 2002 with that of historical data at all sites together revealed that there was no significant change in evenness (historic mean = 0.51 ± 0.02 , 2002 mean = 0.49 ± 0.02 ; pairwise *t* test, $t = 0.78$, $df = 21$, $P = 0.44$). Furthermore, within each of the three regions, Pielou's evenness remained the same (pairwise *t* test, southern California mainland $t = 0.70$, $df = 6$, $P = 0.50$; southern California Channel Islands $t = 0.67$, $df = 9$, $P = 0.52$; central/northern California $t = 0.56$, $df = 4$, $P = 0.61$). Trends in evenness, in addition to species abundance curves, for both historical and 2002 data for six sites (Fig. 3) demonstrate that when Pielou's evenness remained the same or increased in 2002, the species present were in more equal relative abundances than they were historically. More important, data indicate that many of the rare species found in the past are now absent, with more common species usually in lower abundances. In some cases, large numbers of barnacles skew the 2002 data, resulting in

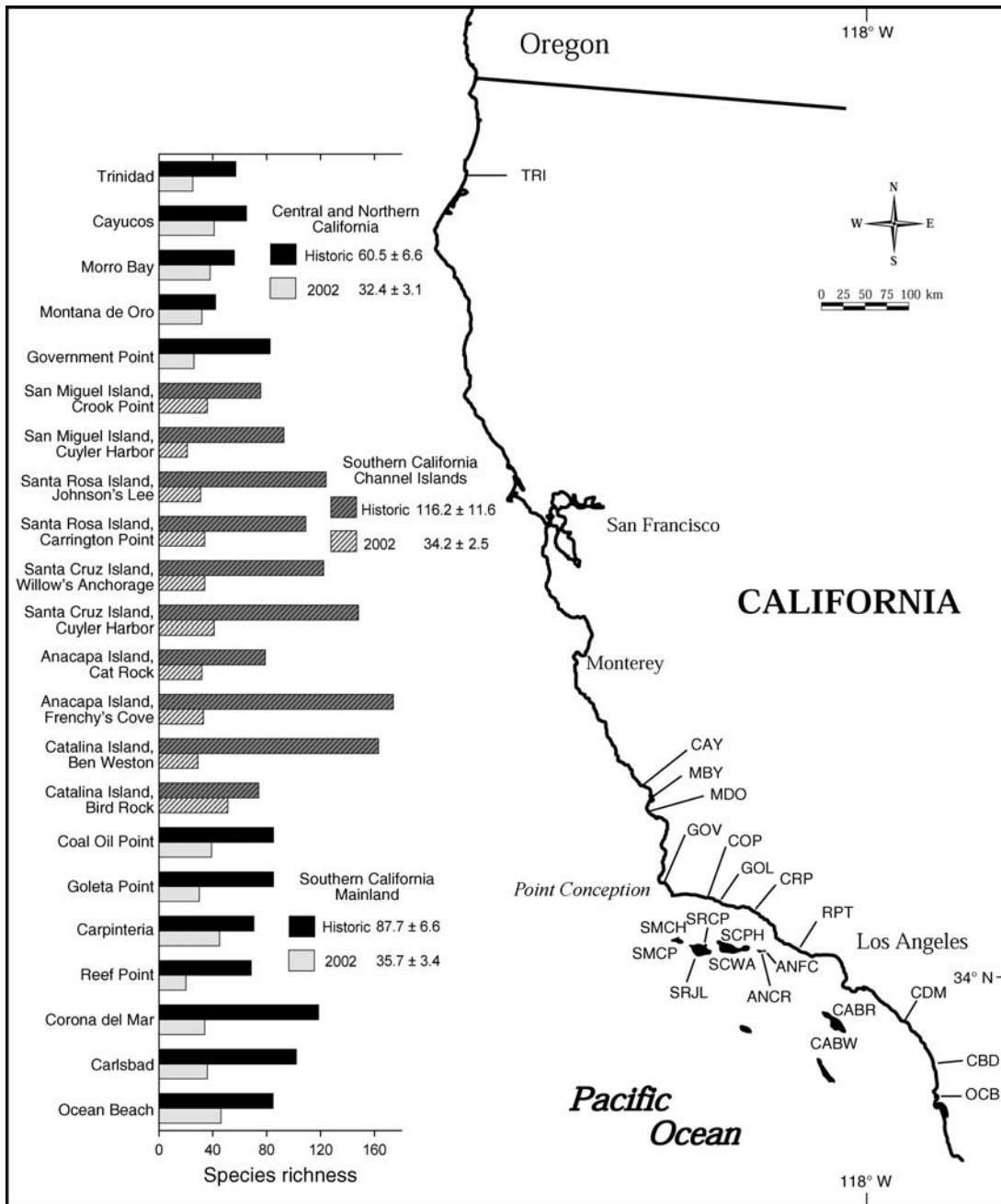


FIG. 1. Total invertebrate richness measured at 22 sites along the California coast, comparing historical richness with that measured in 2002. Richness was measured from pooled invertebrate counts in five 0.03-m² plots (0.15 m² total), except at Trinidad, where diversity was measured in a 0.06-m² area. Means (±SE) are reported for three regions: southern California mainland, southern California Channel Islands, and central/northern California, USA.

lower evenness (Fig. 3). Pielou's evenness in the 1970s also were often skewed by a few species in very high numbers, such as the small bivalve *Lasea subviridis*, whose densities were often >100 000 individuals/m². In 2002, *L. subviridis* was often absent, and when present, never in such large numbers (65–2000 individuals/m²).

The decline in the number of species sampled in mussel beds cannot be explained by differences in

taxonomic resolution. Although not all invertebrates were identified to species, different morphospecies were distinguished from each other and given a species number. The main taxonomic uncertainty encountered was the identification of polychaetes and ectoprocts, which have very fine-scale differences among species. Species lists, mostly presence/absence lists, were presented for 15 of the 22 sites with historical richness data.

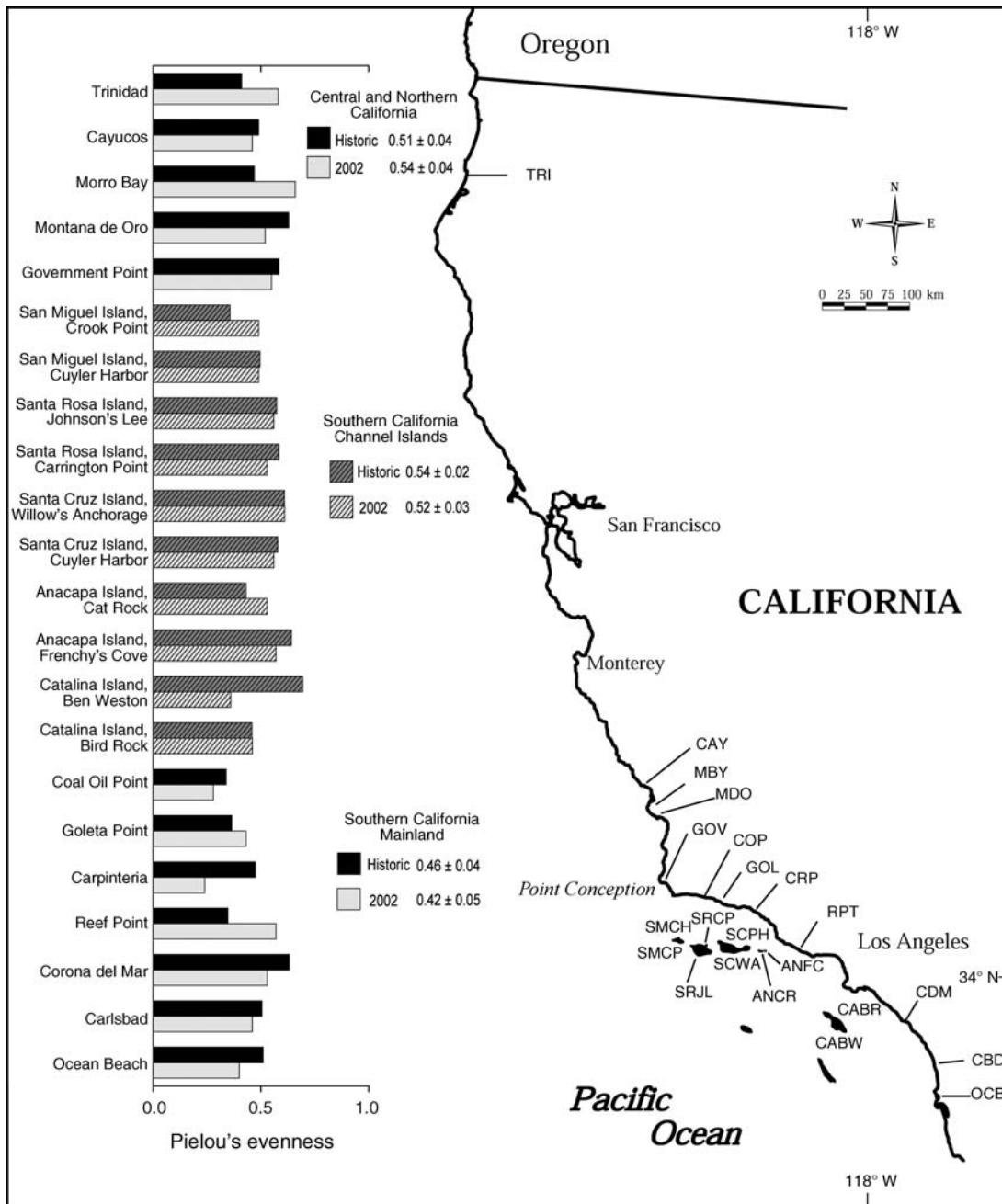


FIG. 2. Pielou's evenness calculated from densities of invertebrates measured at 22 sites along the California coast, comparing historical evenness with that measured in 2002. Evenness was measured from pooled invertebrate counts in five 0.03-m² plots (0.15 m² total), except at Trinidad, where evenness was measured in a 0.06-m² area. Means (± se) are reported for three regions: southern California mainland, southern California Channel Islands, and central/northern California.

Polychaetes at these sites made up a large portion of the richness found in the past (26 of 80 species, ~32%). In 2002, polychaetes still made up a relatively large portion of the richness (6 of 35 species, ~17%) but were much lower in number. To account for possible errors in identification of polychaetes and ectoprocts, we removed them from present and historical data (Fig. 4). Many sites currently did not have polychaetes or ectoprocts or,

if so, they were present in very small numbers (5–20 individuals in pooled 0.15-m² cores in 2002 as compared to 350–1500 individuals in pooled 0.15-m² cores in 1978 at six sites where previous abundances were reported). Therefore, removing a large number of species from richness data reported in the past as compared to removing the small amount of error that might have skewed the current data is a very conservative approach.

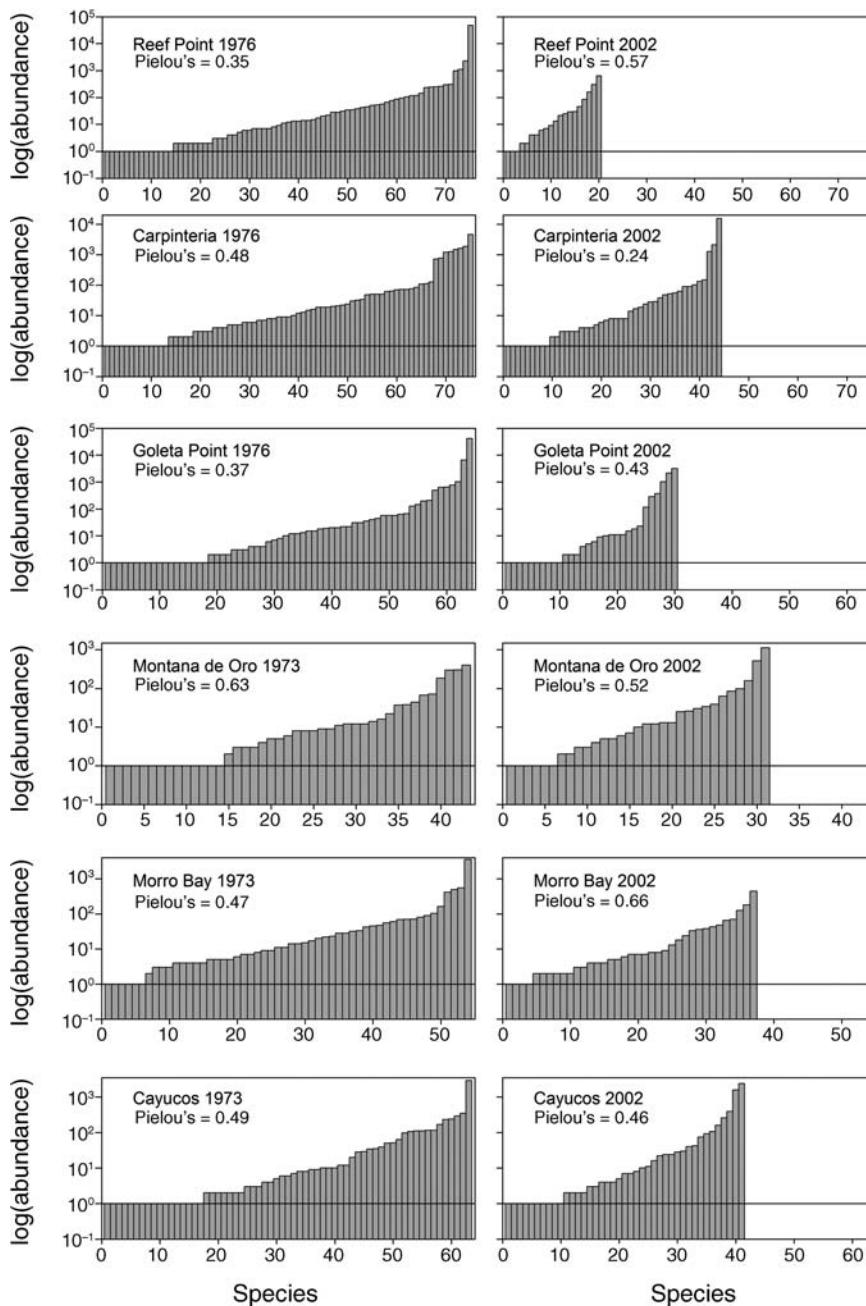


FIG. 3. Abundance curves (log-transformed) for species found within five pooled 0.03-m² plots (0.15 m² total) from historical data and data obtained in 2002 at six sites. Species are ordered from lowest to highest abundance.

Even after removal of these species, there was a consistent decline in total species richness at all sampled sites. At only these 15 sites, an original mean richness of 79.8 in the 1970s and 34.3 in 2002 was reduced by removing polychaetes and ectoprocts to 57.8 and 28.7, respectively, and richness was still significantly lower in 2002 (pairwise *t* test on log-transformed data, *t* = 6.0, *df* = 14, *P* < 0.001).

DISCUSSION

Rapid population declines and loss of biological diversity is occurring at an alarming rate worldwide. Examples of biodiversity loss and extinction continue to be documented (e.g., Brook et al. 2003, Thomas et al. 2004b). We also observed large declines in species richness in northeastern Pacific mussel bed communities. Species loss occurred at all 22 sites sampled across a

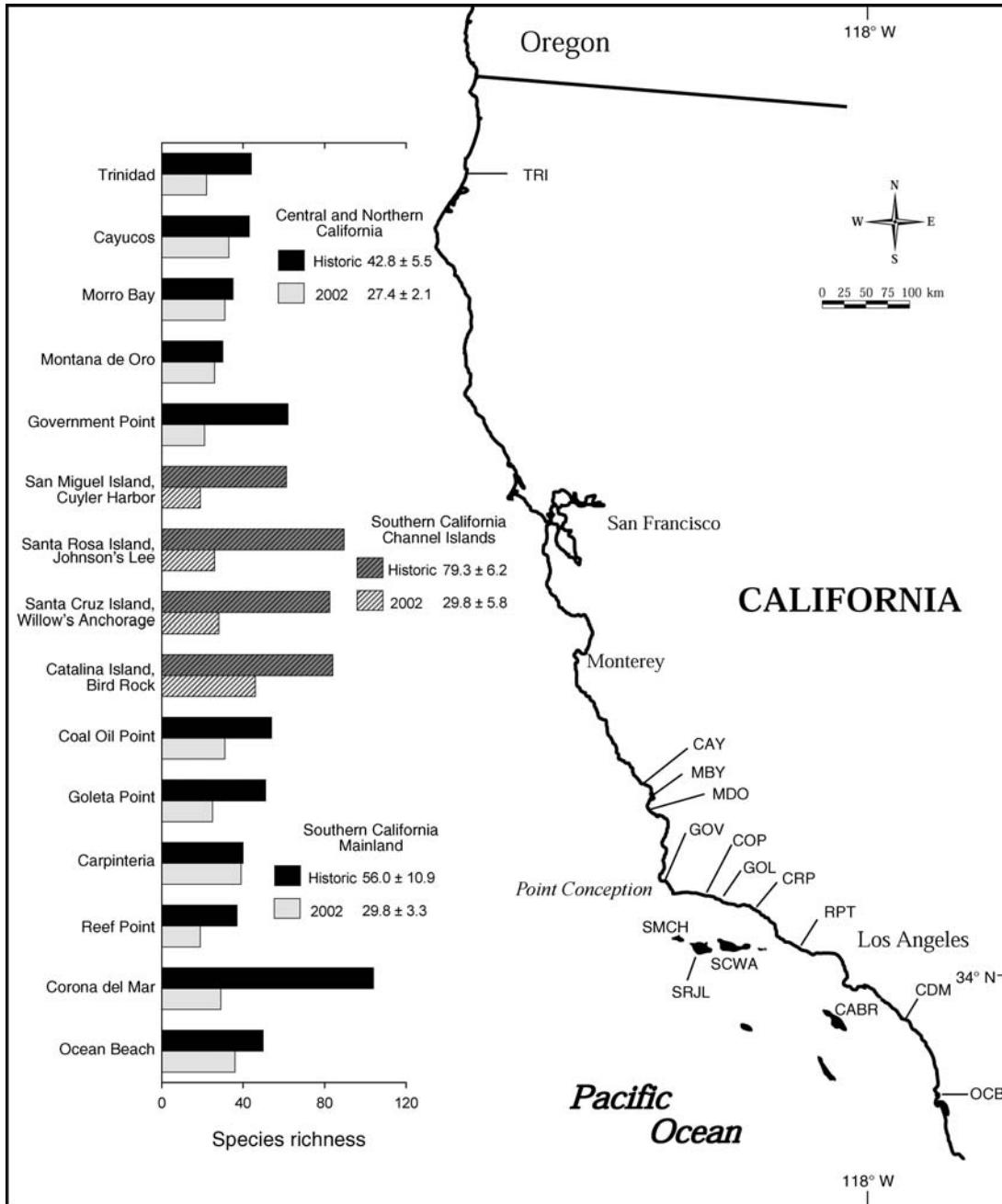


FIG. 4. Total invertebrate richness after removing the species richness of polychaetes and ectoprocts within five 0.03-m² plots (0.15 m² total) at 15 sites along the California coast, comparing historical richness with that measured in 2002. Means (±SE) are reported for three regions.

large geographic range (~1300 km), particularly within the southern portions of California. The reasons for declines in mussel bed diversity over the past few decades were not investigated in this study but are discussed.

Rapid contemporary diversity loss and extinction in other systems are usually driven by human activities, in particular habitat degradation or loss (Wilson 1985). In

the ocean, diversity loss and habitat destruction are commonly documented in coral reef ecosystems (e.g., Jackson et al. 2001). Similar losses in diversity have been observed in terrestrial systems; for example, mass extinction and biodiversity loss for a wide range of taxa in Singapore are related to a 95% loss in forest habitat over the last two centuries (Brook et al. 2003). In mussel communities, destruction or degradation of the mussel

bed matrix would be expected to result in community diversity loss. Mussel bed diversity has been shown to be related to the complexity of a mussel bed (Kanter 1977), and statistically and positively correlated with mussel bed thickness or mussel biomass (Kanter 1979, Smith 2005) and amount and type of trapped sediment within a bed (Straughan and Kanter 1977, Straughan 1978, Kanter 1979). Therefore, we expected the large declines in mussel community diversity to be directly related to declines in mussel bed complexity, mussel biomass, or mussel bed thickness. This was not the case, however. Mussel biomass and thickness measured concurrently with biodiversity did not exhibit consistent declines along the California coast (Smith 2005). Mussel biomass declined at three southern California sites but remained the same at another site in southern California and at two northern California sites (Smith 2005). Mussel bed thickness also showed trends of declines at six of 10 sites in southern California but remained the same or increased in four central and northern California sites; a regression between change in richness and change in thickness was not significant ($r^2 = 0.07$, $P = 0.35$). Therefore declines in richness of mussel communities could not be explained solely by destruction or degradation of the mussel bed habitat.

Since declines were consistent over a large spatial scale, it is clear that local phenomena such as human use or pollution were not solely responsible. Recreational use of the rocky intertidal zone is known to cause declines in mussels (Smith 2005, Smith and Murray 2005) and in other target flora and fauna (Murray et al. 1999, Ambrose and Smith 2005). However, sites sampled in this study varied greatly in the degree of human use (Smith 2005), including sampled sites with no human visitation. Similarly, pollution is known to cause deleterious effects to intertidal organisms (e.g., Littler and Murray 1975), but is unlikely the sole factor in diversity declines, since pollution levels undoubtedly varied greatly among sampled sites. For example, the offshore Channel Islands in southern California have lower levels of contaminants compared to mainland areas (Alexander and Young 1976), yet biodiversity showed the largest decline on the islands. In addition, most pollutants in southern California, and likely central and northern California, have decreased markedly since the early 1970s (Schiff et al. 2000). Therefore declines in community richness occurred after pollutant levels had decreased. Although these factors may play a role in diversity reduction at some sites, they cannot explain the dramatic and consistent patterns of richness declines observed over a large geographic scale.

We suggest that observed mussel community diversity has declined in response to changes in regional climate over the past 30 years. A climate regime shift toward warmer temperatures occurred in the north Pacific Ocean in 1976 (Miller et al. 1994). Following the 1976 Pacific Decadal Oscillation (PDO) shift, sea surface temperatures (SSTs) increased, followed by an increase

in stratification that isolated the deeper nutrient-rich layers, resulting in decreased productivity. For example, in southern California, productivity declines associated with regional climate change were documented indirectly by an 80% decline in zooplankton biomass between 1951 and 1993 (Roemmich and McGowan 1995). In central and northern California, production declines were not as clearly documented as that of southern California because of the lack of direct, long-time series data. However, evidence suggests that declines occurred: low frequency (interannual and longer) changes in plankton have correlated well with zooplankton changes observed in southern California (McGowan et al. 1996) in addition to a marked increase in thermocline depth (Oedekoven et al. 2001). The PDO shift and subsequent warming trend and shift in oceanic processes appeared to continue through the late 1990s (McGowan et al. 2003) but others have argued that a shift toward a cold-water regime may have begun in 1998 (Schwing et al. 2002, Venrick et al. 2003). Oceanographic evidence suggests a trend of decreasing SST and increasing offshore productivity from 1998–2004, but temporal and spatial variations and possible El Niño/La Niña conditions have left a great deal of uncertainty about whether there has been a cold-water regime shift. Despite a potential shift toward more favorable oceanic conditions, it has not resulted in a long-term cold water regime with high productivity as was present before the 1976 PDO shift. Since historical mussel community data were collected from studies conducted from 1968 to 1977, they most likely reflect mussel communities prior to the effects of the regime shift in 1976. In addition, since current mussel community data were collected in 2002, before a clear shift to a colder regime and prior to any long-term productivity increases, they likely reflect mussel communities during an unfavorable period.

We suggest a link between mussel bed biodiversity and ocean productivity. However, it is unclear whether these declines are a result of the natural PDO cycle or a long-term trend from anthropogenically driven global warming. Because the ocean waters of the Pacific have historically oscillated between cold- and warm-water regimes, there is much discussion about whether the warm regime experienced from the 1970s to the late 1990s, and perhaps longer, are part of a natural cycle that will eventually shift toward a colder-water, more productive state. If so, we would expect mussel bed biodiversity to recover with time after more favorable, productive ocean waters return. If changing ocean conditions are part of a global trend of anthropogenically driven warming, then the observed declines may be part of a long-term downward trend.

Global and regional climate change resulting in warmer ocean temperatures are widely predicted and documented to cause shifts in the distribution of species toward the poles, with increased abundances of warm-water species (Lubchenco et al. 1993, Parmesan and

Yohe 2003). For instance, in a rocky intertidal zone in California, 10 of 11 southern invertebrate species increased in abundance while five of seven northern species decreased (Sagarin et al. 1999), presumably due to ocean warming. With only a limited amount of historical data reporting species abundance, we did not observe any clear patterns of increases in warm-water species or decreases in cold-water species. Instead, we observed an overall decline in abundance of most species. Furthermore, our ability to detect shifts in species range was limited, as very few of the species found were near their northern or southern limits. The sites sampled were not considered to be biogeographic breaks where potential range shifts could be detected.

Recently several researchers have proposed that ocean warming may result in cascading community changes, such as decreases in the abundance of higher trophic-level species due to changes in ecological interactions and biological processes instead of, or in addition to, shifts in species ranges (Viet et al. 1996, Holbrook et al. 1997, Viet et al. 1997, Hyrenback and Viet 2003, Schiel et al. 2004). The large decline in productivity in California coastal waters over the past 30 years is of particular interest. Patterns of decline in the abundance of pelagic sea birds, fish, and invertebrates are paralleled by, and suggested to be linked to, concurrent declines in productivity (Viet et al. 1996, Holbrook et al. 1997, Viet et al. 1997, Hyrenback and Viet 2003, Schiel et al. 2004). Similarly we observed declines in abundance of many invertebrates within mussel beds over the same period in which productivity declines were documented. The causal link between declines of various faunal groups is unknown but suggested to be linked to reductions in food supply cascading across all trophic levels (e.g., Holbrook et al. 1997). Our data also suggest that the decline is spread throughout all community members at all trophic levels, as there were no differences in changes of particular groups of species (e.g., filter feeders, grazers, predators).

The potential for global or regional climate change to cause reductions in biodiversity and local extinctions has been discussed repeatedly using modeling (Peterson et al. 2002, Roberts et al. 2002, Thomas et al. 2004a). Global meta-analysis predicts that, on the basis of midrange climate warming for 2050, 15–37% of species in sampled terrestrial taxa will become extinct (Thomas et al. 2004a). Modeling in certain regions or habitats also predicts similar declines, such as an approximate 30% decline in biodiversity in birds, mammals, and butterflies in Mexico (Peterson et al. 2002). In tropical reefs, 7–54% of reef fishes, coral, and other invertebrates are vulnerable to extinction (Roberts et al. 2002).

Although many predictions are made for biodiversity declines, few examples exist. Our study provides evidence that declines in productivity associated with regional climate change may be linked to declines in biodiversity in intertidal mussel communities, as abundances of most species declined with rare species disappearing. Declines in biodiversity linked to the Pacific Decadal Oscillation

shift toward warmer temperatures was also observed in reef fishes in southern California, with richness declines between 15% and 25%, synchronous with climate change-induced declines in zooplankton (Holbrook et al. 1997). It has been well documented that local variations in productivity can drive community structure (Menge et al. 1997) and affect species richness (MacLeod et al. 2004), but little evidence has been presented on a larger spatial scale or linked to warming oceanic water. Our study suggests that warming ocean waters and warming-induced declines in productivity can cause regional declines in biodiversity.

ACKNOWLEDGMENTS

This project was partially funded by the Environmental Protection Agency (EPA) and the Minerals Management Service through the Coastal Marine Institute at the University of California, Santa Barbara. We thank the following for help in accessing sites: Daniel Richards, Derek Lerma, and the Channel Islands National Park; Lyndal Laughrin and the Santa Cruz Island UC Reserve; Kathy Ann Miller and the USC Wrigley Marine Science Center, Mike Wells and the Carlsbad State Beach; Peter Raimondi and Melissa Wilson; Bixby Ranch; Cristina Sandoval and the Coal Oil Point UC Reserve; Virginia Gardner and Carpinteria State Beach; and Don Canestro and the Rancho Marino UC Reserve. We also thank William Hamner and two anonymous reviewers for helpful comments.

LITERATURE CITED

- Alexander, G. V., and D. R. Young. 1976. Trace metals in southern California mussels. *Marine Pollution Bulletin* 7:7–9.
- Ambrose, R. F., and J. R. Smith. 2005. Restoring rocky intertidal habitats in Santa Monica Bay. Technical Report for the Santa Monica Bay Restoration Commission, Los Angeles, California, USA.
- Bengtsson, J., H. Jones, and H. Setälä. 1997. The value of biodiversity. *Trends in Ecology and Evolution* 12:334–336.
- Brook, B. W., N. S. Sodhi, and P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* 424:420–423.
- Cimberg, R. L. 1975. Zonation, species diversity, and redevelopment in the rocky intertidal near Trinidad, northern California. Thesis. Humboldt State University, Humboldt, California, USA.
- Grime, J. O. 1997. Biodiversity and ecosystem function: the debate deepens. *Science* 277:1260–1261.
- Holbrook, S. J., R. J. Schmitt, and J. S. Stephens. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications* 7:1299–1310.
- Hyrenbach, K. D., and R. R. Viet. 2003. Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales. *Deep-Sea Research II* 50:2537–2565.
- Jackson, J. B. C. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637.
- Kanter, R. G. 1977. Structure and diversity in *Mytilus californianus* (Mollusca: Bivalvia) communities. Dissertation. University of Southern California, Los Angeles, California, USA.
- Kanter, R. G. 1978. Intertidal study of the Southern California Bight. 1.2: Mussel communities. Volume III. U.S. Bureau of Land Management, Department of the Interior, Los Angeles, California, USA.
- Kanter, R. G. 1979. Intertidal study of the Southern California Bight. 7.0: Mussel community studies. Volume II. U.S. Bureau of Land Management, Department of the Interior, Los Angeles, California, USA.

- Kanter, R. G. 1980. Biogeographic patterns in mussel community distribution from the Southern California Bight. Pages 341–355 in D. M. Power, editor. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.
- Littler, M. M., and S. N. Murray. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology* **30**:277–291.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- Lubchenco, J., S. A. Navarrete, B. N. Tissot, and J. C. Castilla. 1993. On possible ecological responses to global climate change: nearshore benthic biota of Northeastern Pacific coastal ecosystems. Pages 147–166 in H. A. Mooney, E. R. Fuentes, and B. I. Kronberg, editors. Earth system response to global change. Academic Press, New York, New York, USA.
- MacLeod, C. D., N. Hauser, and H. Peckham. 2004. Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. *Journal of the Marine Biological Association of the United Kingdom* **84**:469–474.
- McGowan, J. A., S. J. Bograd, R. J. Lynn, and A. J. Miller. 2003. The biological response to the 1977 regime shift in the California Current. *Deep-Sea Research II* **50**:2567–2582.
- McGowan, J. A., D. B. Chelton, and A. Conversi. 1996. Plankton patterns, climate, and change in the California Current. *California Cooperative Oceanic Fisheries Investigations Reports* **37**:45–68.
- Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnology and Oceanography* **42**:57–66.
- Miller, A. J., D. R. Cayan, T. P. Barnett, N. E. Graham, and J. M. Oberhuber. 1994. The 1976–77 climate shift of the Pacific Ocean. *Oceanography* **7**:21–26.
- Murray, S. N., T. G. Denis, J. S. Kido, and J. R. Smith. 1999. Human visitation and the frequency and potential effects of collecting on rocky intertidal populations in southern California marine reserves. *California Cooperative Oceanic Fisheries Investigations Reports* **40**:100–106.
- Naeem, S., L. J. Thompson, S. P. Lowler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–737.
- Oedekoven, C. S., D. G. Ainley, and L. B. Spear. 2001. Variable responses of seabirds to change in marine climate: California Current, 1985–1994. *Marine Ecology Progress Series* **212**:265–281.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37–42.
- Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier, and D. R. B. Stockwell. 2002. Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**:626–629.
- Pimm, S., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* **269**:347–350.
- Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. *Between Pacific tides*. Stanford University Press, Stanford, California, USA.
- Roberts, C. M., C. J. McClean, J. E. N. Veron, J. P. Hawkins, G. R. Allen, D. E. McAllister, C. G. Mittermeier, F. W. Schueler, M. Spalding, F. Wells, C. Vynne, and T. B. Werner. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**:1280–1284.
- Roemmich, D., and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the California Current. *Science* **267**:1324–1326.
- Sagarin, R. D., J. P. Barry, S. E. Gilman, and C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* **69**:465–490.
- Sala, O. R. et al. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770–1774.
- Schiel, D. R., J. R. Steinbeck, and M. S. Foster. 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* **85**:1833–1839.
- Schiff, K. C., M. J. Allen, E. Y. Zeng, and S. M. Bay. 2000. Southern California. *Marine Pollution Bulletin* **41**:76–93.
- Schulze, E. D., and H. A. Mooney. 1993. *Biodiversity and ecosystem function*. Springer, Berlin, Germany.
- Schwing, F. B. et al. 2002. The state of the California Current, 2001–2002: will the California Current system keep its cool, or is El Niño looming? *CalCOFI Reports* **43**:31–68.
- Smith, F. D. M., R. M. May, R. Pellow, T. H. Johnson, and K. S. Walter. 1993. Estimating extinction rates. *Nature* **364**:494–496.
- Smith, J. R. 2005. Factors affecting geographic patterns and long-term change of mussel abundances (*Mytilus californianus* Conrad) and bed-associated community composition along the California coast. Dissertation. University of California, Los Angeles, California, USA.
- Smith, J. R., and S. N. Murray. 2005. The effects of bait collection and trampling on a southern California *Mytilus californianus* Conrad bed. *Marine Biology* **146**:699–706.
- Straughan, D. 1978. Analysis of mussel (*Mytilus californianus*) communities in areas chronically exposed to natural oil seepage. Prepared for American Petroleum Institute, Washington, D.C., USA.
- Straughan, D., and R. G. Kanter. 1977. Southern California baseline study: mussel community study. Volume III. Report 2.2. Bureau of Land Management, Department of the Interior, Washington, D.C., USA.
- Suchanek, T. H. 1979. The *Mytilus californianus* community: studies on the composition, structure, organization, and dynamics of a mussel bed. Dissertation. University of Washington, Seattle, Washington, USA.
- Suchanek, T. H. 1992. Extreme biodiversity in the marine environment mussel bed communities of *Mytilus californianus*. *Northwest Environmental Journal* **8**:150–152.
- Thomas, C. D. et al. 2004a. Extinction risk from climate change. *Nature* **427**:145–148.
- Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke, and J. H. Lawton. 2004b. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**:1879–1881.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* **294**:843–845.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**:718–720.
- Venrick, E. et al. 2003. The state of the California Current, 2002–2003: tropical and subarctic influences vie for dominance. *CalCOFI Reports* **44**:28–60.
- Viet, R. R., J. A. McGowan, D. G. Ainley, T. R. Wahl, and P. Pyle. 1997. Apex marine predator declines ninety percent in association with changing ocean climate. *Global Change Biology* **3**:23–28.
- Viet, R. R., P. Pyle, and J. A. McGowan. 1996. Ocean warming and long-term change in pelagic bird abundance within the California current system. *Marine Ecology Progress Series* **139**:11–18.
- Wilson, E. O. 1985. The biological diversity crisis: a challenge to science. *Issues in Science and Technology* **2**:20–29.