

# REPORTS

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## TEN YEARS OF INDUCED OCEAN WARMING CAUSES COMPREHENSIVE CHANGES IN MARINE BENTHIC COMMUNITIES

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**Abstract.** One of the most commonly predicted effects of global ocean warming on marine communities is a poleward shift in the distributional boundaries of species with an associated replacement of cold-water species by warm-water species. However, these types of predictions are imprecise and based largely on broad correlations in uncontrolled studies that examine changes in the distribution or abundances of species in relation to seawater temperature. Our study used an 18-year sampling program in intertidal and subtidal habitats and before–after, control–impact analyses. We show that a 3.5°C rise in seawater temperature, induced by the thermal outfall of a power-generating station, over 10 years along 2 km of rocky coastline in California resulted in significant community-wide changes in 150 species of algae and invertebrates relative to adjacent control areas experiencing natural temperatures. Contrary to predictions based on current biogeographic models, there was no trend toward warmer-water species with southern geographic affinities replacing colder-water species with northern affinities. Instead, the communities were greatly altered in apparently cascading responses to changes in abundance of several key taxa, particularly habitat-forming subtidal kelps and intertidal foliose red algae. Many temperature-sensitive algae decreased greatly in abundance, whereas many invertebrate grazers increased. The responses of these benthic communities to ocean warming were mostly unpredicted and strongly coupled to direct effects of temperature on key taxa and indirect effects operating through ecological interactions.

**Key words:** BACI analysis; benthic community structure; biogeographic distribution information; climate change, predicting effects; Diablo Cove, California, USA; ocean warming; rocky reef; temperature change; thermal discharge of a power plant, effects.

### INTRODUCTION

Ocean warming through climate change is expected to have significant effects on the composition and structure of marine communities (Fields et al. 1993). These include changes in distributional boundaries of species and replacement of cold-water taxa by others with warm-water affinities. Paleoclimatic records showing shifts in the distribution or abundance of species associated with changes in temperature (Kennett and Stott 1991), localized changes in species abundances over decades (Southward et al. 1995, Holbrook et al. 1997, Sagarin et al. 1999), and changes associated with El Niño–Southern Oscillation events (Pearcy and Schoener 1987, Dayton et al. 1999) support such scenarios. However, evidence for changes due to ocean warming is limited and based largely on correlations

between natural changes in seawater temperature and species' occurrences or abundances (Lubchenco et al. 1993), or else on point counts separated by large time periods (e.g., Sagarin et al. 1999). Few empirical studies incorporate significant changes in seawater temperature over periods long enough to span the lives of most species, while also having control areas and continuous time series of sampling that allow specific spatial and temporal trends in community structure to be detected and tested.

Here, we address the hypothesis that elevated seawater temperature brought about by the thermal discharge of a power generating station in California underlay changes to rocky intertidal and subtidal communities. Eighteen years of sampling before and after the thermal discharge began, and the simultaneous sampling of nearby control areas that experienced only natural temperatures, allowed a robust assessment of changes in species' abundances through time. The sustained elevation of seawater temperature enabled an

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exceptionally strong and direct test of responses by nearshore benthic marine communities to ocean warming. Furthermore, the study area was close to a source of potential invaders because it is only 138 km north of Point Conception, a recognized boundary between a warm-temperate biota to the south and a cool-temperate biota to the north (Ricketts et al. 1985).

#### METHODS

Diablo Cove is on an exposed rocky coast in central California, USA (35°12' N, 120°52' W), has a shoreline ~2 km long, a surface area of 15 ha, an average depth of 8 m, and a maximum depth of 18 m. The nearby power plant draws seawater from outside the cove, uses it in a cooling system to re-condense freshwater steam, and discharges it into the cove at a maximum rate of  $9.5 \times 10^9$  L/d, creating a thermal plume that spreads throughout the cove. The plant has operated at mostly full power since May 1985 and very little is discharged other than heated water. Required regular water monitoring and bioassays showed that concentrations of other constituents were very low relative to the large volume of the discharge and did not present acute or chronic toxicity to marine larval organisms used in the tests. Temperature was recorded continuously (every 20 min) from 1976 with digital recorders ( $\pm 0.2^\circ\text{C}$  accuracy) in metal canisters at the -3 m MLLW level (3 m below mean lowest low water) of several stations.

Biological surveys were done six times each year from 1978 through 1988 and four times annually from 1989 through 1995. There were four intertidal and five subtidal stations within Diablo Cove and two subtidal and three intertidal control stations 1–2 km outside the cove beyond the influence of the discharge. Each intertidal station had two 30 m fixed transects parallel to the shore, one each at the +0.3 m and +0.9 m MLLW tidal levels. Ten 1-m<sup>2</sup> quadrats (initially chosen randomly) per transect were sampled during each survey. All visible algae and invertebrates were counted or their percentage cover assessed. At each subtidal station, a fixed 28-m<sup>2</sup> circular plot divided into four quadrants at a depth of 3 m to 4 m was sampled on each occasion. In each quadrant, understory algal and attached invertebrate cover was estimated from 50 random points, and invertebrates and kelp were counted. The great majority of taxa were identified to species level. Following Sagarin et al. (1999), individual species were classified as “cosmopolitan” (i.e., with an extensive north-south distribution along the west coast), “northern” (with a southern limit north of Point Conception) or “southern” (with a northern limit south of Cape Mendocino) based on information in Morris et al. (1980) and Abbott and Hollenberg (1976). Taxa were excluded from this classification if they were identified only to genus and may have contained species of different geographical affinities.

BACI (before–after, control–impact) analysis of variance using “before” and “after” data from “control”

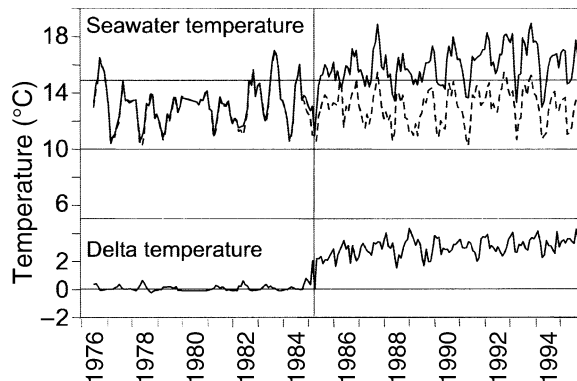


FIG. 1. Monthly mean temperatures at control (dashed line) and impact (solid line) sites measured at a depth of 3 m below MLLW from 1976 to 1995. Delta temperatures are the average differences between control and impact stations. The vertical line at 1985 shows when thermal change began within Diablo Cove.

and “impact” areas was used to detect significant thermal effects (Stewart-Oaten et al. 1986). The “before” period was January 1978 through December 1984 and the “after” period was January 1987 through June 1995. Surveys from January 1985 through December 1986 were omitted to allow time for thermal effects to occur. The high power to detect small changes in abundance was due to the number of replicate surveys in each period. The analytical variable was the difference between the mean of each impact station and the grand mean of all the control stations in each survey. The differences between these paired means (“deltas”) were then compared statistically before and after the putative impact. Data for each species were tested for additivity, linear trend, serial correlation, and homogeneity of variance, transformed appropriately to meet test assumptions, and then analyzed using a two-way ANOVA with factors for “period” and “station.” If the interaction was not significant, “period” was used to test for effects of thermal change. A significant interaction indicated an impact of varying magnitude among stations or no impact due to variable results among stations. For taxa that tested significant, we calculated percentage change in abundance in Diablo Cove relative to controls as: Relative percentage change =  $[(X_{Bc} \div X_{Bi}) - (X_{Ac} \div X_{Ai})] / (X_{Ac} \div X_{Ai}) \times 100$ , where  $X_{Bc}$  = mean abundance at the pooled control sites before thermal increase;  $X_{Bi}$  = mean abundance at the pooled Diablo Cove sites before thermal increase;  $X_{Ac}$  = mean abundance at the pooled control sites after thermal increase;  $X_{Ai}$  = mean abundance at the pooled Diablo Cove sites after thermal increase.

#### RESULTS

Seawater temperatures within and outside Diablo Cove (California, USA) were similar from 1976 to 1985, when the heated discharge began (Fig. 1). However, from 1986 through 1995 they were elevated by

TABLE 1. The number of species and the percentage of all taxa combined that significantly increased (Inc.), decreased (Dec.), or did not change (Nc) in abundance within Diablo Cove (California, USA) relative to control stations outside the cove over the 10 years after the rise in seawater temperature.

Species types	Cosmopolitan			Northern			Southern		
	Inc.	Dec.	Nc	Inc.	Dec.	Nc	Inc.	Dec.	Nc
Intertidal algae	1	15	1	0	1	0	0	1	0
Intertidal invertebrates	11	8	1	1	0	1	2	0	2
Subtidal algae	6	6	2	1	1	0	1	0	0
Subtidal invertebrates	11	16	9	0	1	0	6	3	1
All taxa (%)	26.6	41.3	11.9	1.8	2.8	0.9	8.3	3.7	2.8

Notes: Species were categorized as cosmopolitan, northern, or southern in their biogeographic affinities. Significance was based on BACI analyses (see *Methods*).

an average of 3.5°C inside the cove, with monthly means ranging from 2.0 to 5.1°C above ambient. Maximum temperatures occurred during the El Niño–Southern oscillation (ENSO) years of 1983, 1987, and 1992–1993. The coast in and around Diablo Cove initially had marine communities typical of other semi-protected sites in the region (Ricketts et al. 1985). Intertidal areas were dominated by foliose (e.g., *Mazzaella flaccida*) and branched (e.g., *Chondracanthus canaliculatus*) red algae, with some grazing gastropods and sessile invertebrates in the understory. Subtidal areas had a canopy of northern bull kelp, *Nereocystis luetkeana*, an understory dominated by the kelps *Pterygophora californica* and *Laminaria setchellii*, and primary cover of coralline and foliose red algae, with a lush assemblage of smaller algae and invertebrates interspersed.

During our 18-year study, 714 taxa were counted or assessed for percentage cover, but only 172 species

were sufficiently abundant to be analyzed statistically. Of these, 150 species (87%) changed significantly in abundance at stations with elevated temperatures relative to control stations, with 65 species (37.8%) increasing and 85 species (49.4%) decreasing.

The biogeographic affinities of 109 of the 172 species could be assigned with confidence (see Appendix). There was no consistent pattern of change in abundances related to geographic affinities (Table 1). Most intertidal algae (89%) were cosmopolitan. Of these, 15 species decreased in abundance, as did the one northern and one southern algal species. Twenty of the 26 intertidal invertebrate species (77%) were cosmopolitan, and 11 species increased, eight species decreased, and one species remained unchanged relative to controls. The few northern and southern species had equal numbers increasing or showing no change. Most subtidal algae (82%) were cosmopolitan, with six species increasing, six species decreasing, and two species remaining unchanged in abundance. One northern species increased and one decreased, while the only southern species increased. Thirty-six of the 47 subtidal invertebrates (77%) were cosmopolitan, of which 11 species increased, 16 species decreased, and nine species had no change. The one northern species decreased, while six southern species increased, three species decreased, and one species remained unchanged. Overall, of the 80% of species that were cosmopolitan, far more decreased (41.3%) than increased or remained unchanged. Of the 6% of species that were northern, more decreased (2.8%) than increased (1.8%). And of the southern 15% of species, more increased (8.3%) than decreased (3.7%).

Most species within Diablo Cove underwent large relative changes in abundance in the 10 years following seawater warming. Fifty-four percent of algae (Fig. 2A) and 27% of invertebrates (Fig. 2B) declined by at least 50%. Dominant algae (with an initial combined cover >60%) declined dramatically, especially the cosmopolitan red algae *Mastocarpus papillatus* (−65%) in the upper zone, *Endocladia muricata* (−63%), *Mazzaella flaccida* (−98%), and *Chondracanthus canaliculatus* (−51%). Algal taxa richness declined by 40%.

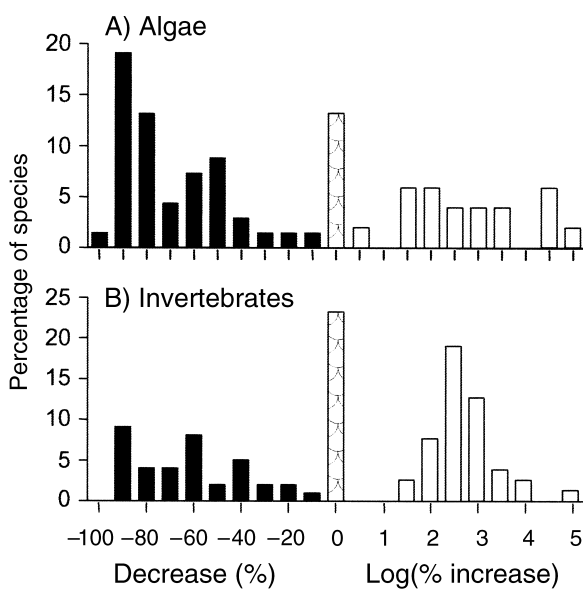


FIG. 2. Percentage changes in abundance of (A) algae and (B) invertebrate species relative to controls after thermal change, shown as decreases (solid bars), no change (mottled bars), and  $\log_{10}$  increases (open bars).

In contrast, non-calcified algal crusts increased by 62%. The few other increases were in cosmopolitan taxa that, taken together, comprised  $\leq 1\%$  of total algal cover.

Subtidal understory kelps declined by 82% from an average of 7.3 to 1.3 plants/m<sup>2</sup>. The initially abundant cosmopolitan kelps *P. californica* and *L. setchellii* declined by  $\sim 90\%$ , but a cosmopolitan understory red alga, *Cryptopleura violacea*, increased by 3000% (i.e., a log percentage increase of 3.47) to cover 30–50% of the substratum. Some of the most important changes involved the large kelps. *N. luetkeana* declined by 97% in the cove and was replaced by the initially rare southern giant kelp *Macrocystis pyrifera*, which dominated the surface canopy with an average density of 1.5 plants/7 m<sup>2</sup> after 10 years.

Intertidal grazers became very abundant, especially the cosmopolitan *Tegula funebris*, which increased by 79% to a 10-year average of 175 individuals/m<sup>2</sup> on the upper shore, and the cosmopolitan limpet *Macclintockia scabra* that increased by  $>400\%$  to 86 individuals/m<sup>2</sup>. Some initially rare species became common, including limpets of the cosmopolitan genus *Lottia*, which increased from  $\sim 3$  to 9 limpets/m<sup>2</sup>, and the cosmopolitan keyhole limpet *Fissurella volcano*, which increased by  $>700\%$  to 13 limpets/m<sup>2</sup> on the lower shore. The cosmopolitan sea urchin *Strongylocentrotus purpuratus* increased by 3000% to 8.2 individuals/m<sup>2</sup> in the low intertidal zone.

Almost all changes were in the abundances of species already present. A few new invertebrates appeared in impact sites after thermal change, but they were never abundant, such as brittle stars *Ophiothrix* spp. (probably southern; from 0 to 1.1 individuals/0.25 m<sup>2</sup>), *Aplysia californica* (cosmopolitan; from 0 to 0.2 individuals/7 m<sup>2</sup>), *Cryptochiton stelleri* (cosmopolitan; from 0 to 0.1 individual/7 m<sup>2</sup>), and *Norrissia norrisi* (southern; from 0 to 0.1 individual/7 m<sup>2</sup>).

Intertidal habitats were greatly modified in Diablo Cove, especially in the vertical layering of algae. All sites initially had a dense cover (70–80%) of foliose algae up to 10 cm thick, with grazing invertebrates interspersed below. At control sites these algae declined around 1985 and grazers increased, most likely as delayed responses to the severe 1983 ENSO (Fig. 3A). However, dense algae returned within two years and by 1995 both algal and grazer abundances were virtually the same as in 1978. At the thermally affected sites, foliose algae also declined in 1985 but did not recover (Fig. 3B). Instead, grazers dominated for 10 years and, as might be predicted given their high densities (cf. Lubchenco and Cubit 1980), this was accompanied by large increases in bare substratum, low-lying ephemeral turf, and thin algal crusts. Other changes, especially at higher tidal levels, were increases in space-occupying species such as barnacles, *Chthamalus fissus* and *Tetraclita rubescens*, and the sand tube worm *Phragmatopoma californica*. Although these species had large percentage increases relative to con-

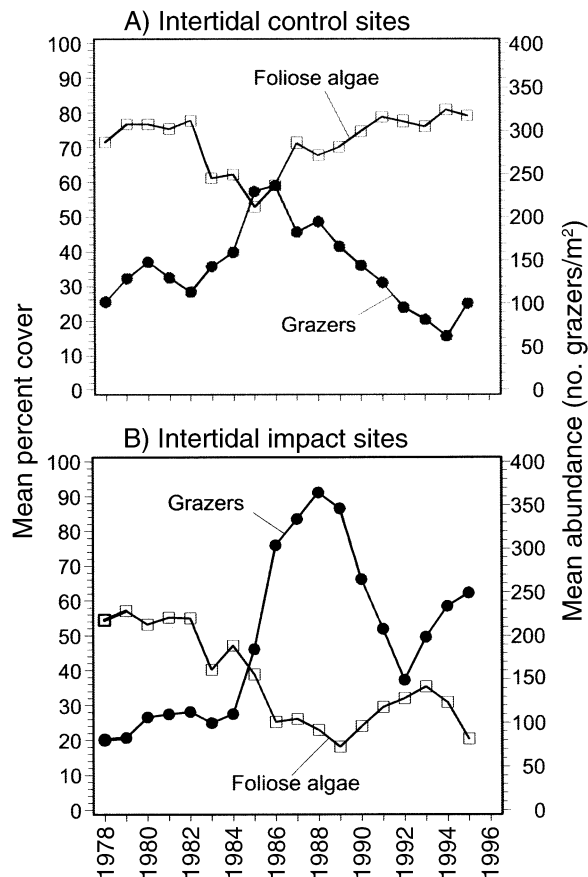


FIG. 3. Annual mean percent cover of foliose algae (open squares; left-hand axis) and abundance of grazers per square meter (solid circles; right-hand axis) in the intertidal zone of (A) control sites and (B) impact sites.

trol areas (7400%, 350%, and 49000%, respectively), their overall abundances remained low. The total cover of all sessile invertebrates increased from  $\sim 2.0$ – $4.7\%$  in the intertidal zone of Diablo Cove sites. There were also slight increases of predatory gastropods such as *Acanthina* spp. and *Ocenebra* spp. on the upper shore, but these were not statistically significant.

Community changes in subtidal habitats were more complex. Control sites (Fig. 4A) had a primary substratum cover of foliose algae from 1978 to 1995 but understory kelps underwent large changes in abundance, ranging from 20 to 225 kelps/m<sup>2</sup>. Kelps had high recruitment after the 1983 and 1987 ENSO events but then gradually declined. Grazers fluctuated in abundance. By the end of the study, however, the control sites looked remarkably similar to their initial condition. The thermally affected sites had far greater changes (Fig. 4B). Bull kelp was replaced by giant kelp, subcanopy kelps declined and had no major episodes of recruitment, and grazers fluctuated and then declined after 1988 as dense foliose algae dominated the substratum. In contrast to control sites, the grazing assemblage changed after 1985 when sea urchins began in-

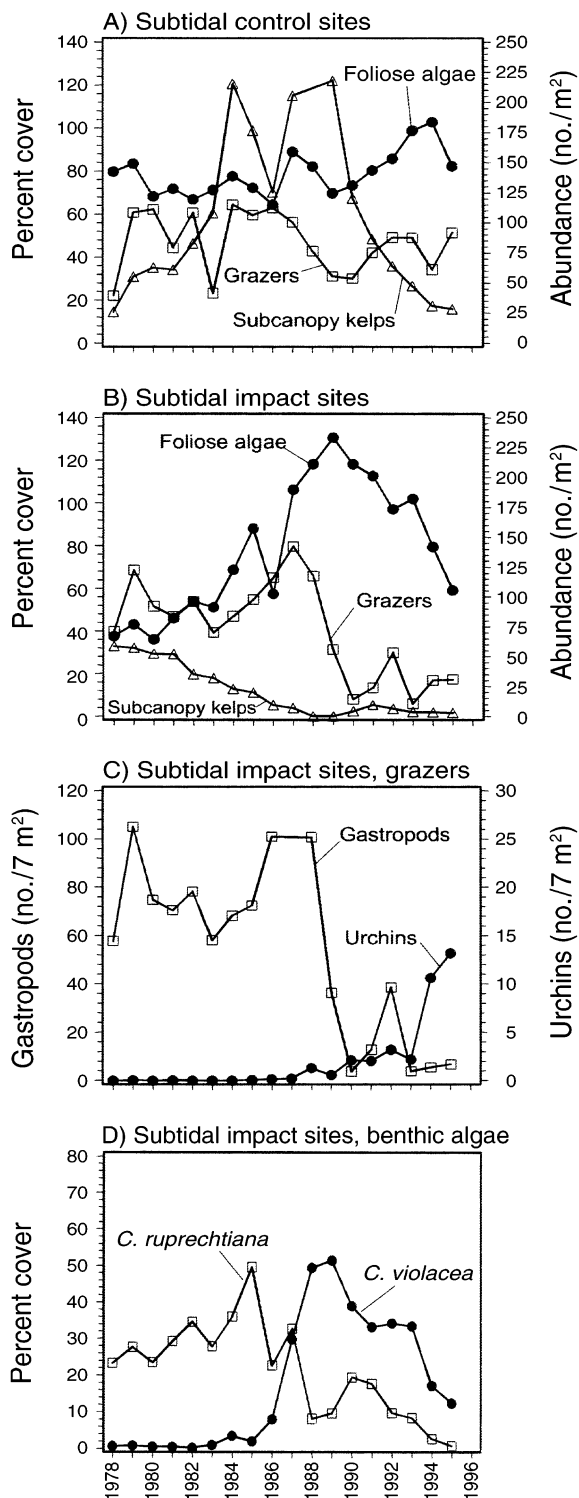


FIG. 4. Annual mean percent cover of foliose algae (left-hand axes) and numbers of subcanopy kelps and grazers (right-hand axes) at (A) subtidal control sites and (B) subtidal impact sites, with (C) a separation of grazers into gastropods and sea urchins, and (D) the percent cover of the two most abundant benthic foliose algae (*Cryptopleura* spp.). Percent cover could total >100% because of layering of algae; the sample area was 7 m<sup>2</sup>.

creasing in abundance while gastropods declined (Fig. 4C). Furthermore, only within Diablo Cove did the dominant benthic algae change (Fig. 4D). The cosmopolitan red alga *Cryptopleura ruprechtiana* was replaced by its cosmopolitan congener *C. violacea*.

DISCUSSION

Key results were that after a sustained rise in seawater temperature the great majority of nearshore species changed in abundance and whole communities changed in character. Mechanisms of change are usually complex, involve the interaction of many factors, and, as abundances change, can be highly sensitive to the strengths of interactions among species (Menge 2000). The level of experimentation (i.e., bay-wide) in this study limits the resolution of the processes responsible for change and, therefore, the sequence of observed changes and their consistency give the best clues for evaluating the processes responsible.

The deterioration of algae clearly preceded increases in grazers. Dominant algae, especially *Mazzaella flaccida*, *Nereocystis*, *Pterygophora*, and *Laminaria*, had acute responses to the increased temperature and declined rapidly, becoming bleached with deteriorating thalli within a few months. This provided new settlement space and an altered light environment to primary substrata (Reed and Foster 1984) and may have triggered a series of responses such as altered mortality, growth, and reproductive and recruitment rates of other species (Ives and Gilchrist 1993), behavioral changes relating to temperature preferences and avoidance (Schroeter et al. 1993, Sanford 1999), and modified food webs and species interactions (Wootton 1993). Initially dominant species had little or no subsequent recruitment, even during the periods when grazer numbers declined (e.g., 1988).

In contrast, grazing gastropods showed a positive response to temperature, which most likely involved physiological tolerances, trophic responses, availability of space and recruitment dynamics. Many intertidal molluscs are highly resistant to the extreme temperatures experienced during low tide and can repair thermal damage to proteins (Tomanek and Somero 1999). Their strong recruitment intertidally was most likely a direct consequence of having more free space to settle after the decline of algae. Once they reached the very high densities seen in Diablo Cove (up to 370 molluscs/m<sup>2</sup>), they would have precluded effective recruitment of macroalgae for much of the post-impact period (Foster 1982). Grazers often recruit into areas cleared of algae along the west coast (Foster et al. 2003), as was seen in all sites after the 1983 ENSO. Given the quick recovery of control sites, however, it is likely that the trophic response of grazing mollusks in the impacted areas was secondary to the direct effects of temperature on algae.

Subtidal changes were more complex. The switch in canopy kelp was predictable because *Nereocystis* was

almost at its southern limit and is intolerant of warm temperatures, whereas *Macrocystis* extends into Mexico. Both species recruited annually but *Nereocystis* juveniles did not survive. The switch in dominance of the two benthic *Cryptopleura* species soon after the temperature change and then their decline were probably responses both to temperature change and to the altered light environment as understory kelps declined and the *Macrocystis* canopy developed. Changes in grazers were complicated. Urchins were initially rare (<0.1 individual/m<sup>2</sup>) in Diablo Cove, but after 1987 aggregated at up to 300 individuals/m<sup>2</sup>. These changes occurred in tandem with overall benthic changes. The abrupt decline of gastropods after 1988 was probably due to predation by fishes known to feed on gastropods such as the sheephead *Semicossyphus pulcher* (Feder et al. 1974) and bat rays, *Myliobatis californica* (Gray et al. 1997). These species were scarce before 1985 but then increased to average abundances of 0.4 and 1.4 individuals per 50 × 5 m transect, respectively, within Diablo Cove while staying at low numbers outside the cove.

Our study provides little support for the hypothesis of predictable directional changes in northern and southern species based on biogeographic models and the metrics used by Sagarin et al. (1999). Although five more southern species increased than decreased, and one more northern species decreased than increased (Table 1), one might have expected that if predictions were robust, the great majority of species within these groups would have exhibited the predicted changes. The utility of the model is also weakened because so few species fell into these categories. Moreover, except for the substitution of giant kelp for bull kelp, the great majority of changes were in widely distributed species, the mortality of which should have been relatively insensitive to variation in temperature. For example, two of the most-affected species (*Mazzaella flaccida* and *Endocladia muricata*) were cosmopolitan and considered to be warm tolerant (Abbott and North 1972), and *Pterygophora* is common in kelp forests of southern California (Dayton et al. 1999), yet all of these virtually disappeared from Diablo Cove. Overall, there were large and unforeseen changes to the benthos that resulted in communities neither typical of sites further south, where warmer seawater temperatures prevail, nor of sites in central California. However, once large changes occurred in dominant algae, some of the community-wide changes became more likely, such as the influx of grazers to the intertidal zone after space became available. It is apparent that biogeographic distribution as defined by current models was a poor predictor of overall changes resulting from warming. Perhaps other measures of species' positions along latitudinal or temperature gradients relative to the range limits for each species may result in more accurate predictions, but such information is currently limited. The problem of characterizing distributions is high-

lighted, for example, by *Fissurella volcano*, which is considered to be a warm-water limpet but was classified as "cosmopolitan" because its range extended just north of Cape Mendocino, while species such as *Lottia pelta* extend to Alaska, so were also cosmopolitan.

The temperatures within Diablo Cove were within the range of those experienced during ENSO events (Glynn 1988) but they were sustained over 10 years. However, they were up to 3 times greater than the natural increase in temperature recorded along the Californian coast over the past 50 years (Roemmich 1992). If ocean warming continues, therefore, our study implies that large and mostly unpredicted changes may occur in nearshore communities. Furthermore, there are potentially greater long-term changes through new invaders and exotic species (Grosholtz 2002), changes in nutrient concentrations and productivity that drive "bottom-up" processes (Roemmich and McGowan 1995, Menge 2000), a rise in sea level, and an increase in extreme storms (Easterling et al. 2000).

Despite uncertainty about the exact mechanisms, the changes themselves were real, lasting, and comprehensive, providing both clues and a caution about predicting effects of climate change. Knowledge of key ecological interactions is necessary but not sufficient to predict changes to communities. Identification of key species and knowledge about their responses to temperature are also necessary. Because of the large number of species present, the resolution of predictions may remain coarse. Our findings highlight that complex and unforeseen impacts can occur in nearshore benthic communities and also caution against using simplified models of species' responses to ocean warming based on their present biogeographic distributions.

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#### APPENDIX

Tables summarizing data used for biogeographic analysis are available in ESA's Electronic Data Archive: *Ecological Archives* E085-051-A1.