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CLIMATE-RELATED CHANGE IN AN INTERTIDAL COMMUNITY OVER SHORT AND LONG TIME SCALES

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Abstract. Changes in the abundance of macroinvertebrate species documented in a rocky intertidal community between surveys in 1931–1933 and 1993–1996 are consistent with the predicted effects of recent climate warming. We resampled 57 0.84-m^2 plots of an intertidal transect first surveyed by W. G. Hewatt at Hopkins Marine Station (HMS), Pacific Grove, California, between 1931 and 1933. Replicating precisely the location of the plots and methodology used by Hewatt, we documented changes in the abundances of 46 invertebrate species, indicating that this intertidal community changed significantly during the 60 yr between surveys. Changes in abundance were related to geographic ranges of species. Most southern species (10 of 11) increased in abundance, whereas most northern species (5 of 7) decreased. Cosmopolitan species showed no clear trend, with 12 increasing and 16 decreasing. Although Hewatt did not record algal species as thoroughly as invertebrates, we were able to document a massive decline in cover of *Pelvetia compressa,* a cosmopolitan fucoid alga that is typically more common in the southern part of its range. Shoreline ocean temperature, taken daily at HMS, warmed by 0.79°C during this 60-yr period, with average summer temperatures up to 1.94°C warmer in the 13 yr preceding our study than in the 13 yr preceding Hewatt's. The hypothesis that climatic warming drove the observed range-related community shifts is supported further by historical records and data from other investigators. Several alternative hypotheses to explain changes in the invertebrate community at HMS, including habitat changes, anthropogenic effects, indirect biological interactions, El Niño–Southern Oscillation (ENSO) events, and upwelling are considered to be less important than climate change. Changes in species' abundances over a short period (3 yr) were relatively small compared to large species shifts over 60 yr and were unrelated to geographic range of the species, indicating that short-term population fluctuations play a relatively minor role in the long-term community changes that we observed.

Key words: climate change; ENSO; geographic range; global warming; invertebrate community structure; long-term study; ocean temperatures; rocky intertidal.

INTRODUCTION

Concern with anthropogenic global climate change has been reflected recently in the ecological literature, with a proliferation of papers on the responses of species and communities to climate change. These studies cover a wide range of natural systems and taxa: terrestrial plants (Davis 1989*a*, Woodward 1992, Beerling 1993), infectious disease (Shope 1991, Patz et al. 1996), insects (Rubenstein 1992), other invertebrates (Bhaud et al. 1995), birds (Root 1993, Taper et al. 1995), freshwater fishes (Scott and Poynter 1991), algae (Breeman 1990), marine fishes (Frank et al. 1990), and coastal marine communities (Fields et al. 1993, Lubchenco et al. 1993, Paine 1993). Most are speculative and offer only predictions of community changes under various climate change scenarios. Almost universally, these authors predict poleward shifts in species' ranges in response to predicted warming trends. Support for this scenario derives from population and community models, or by analogy with biotic responses to past climatological events that share characteristics with expected global climate change (Fields et al. 1993). Pollen abundance in lake sediments, for example, has been used to track vegetation changes over known climatological shifts such as the glacial to interglacial transition beginning 20 000 yr ago (Webb et al. 1987, Davis 1989*a*). Fossil foraminifera from deep-sea sediment have been used similarly to track changes in marine communities (Graham 1992, Webb 1992). By understanding the rates and magnitudes of climatic changes that accompanied these biological changes

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(e.g., through ice core analysis), and by using these data to calibrate Global Circulation Models (GCMs) (e.g., Ruddiman 1990), predictions of biological changes can be made under a variety of climate change scenarios. Nevertheless, paleo-analogies may not be entirely useful for evaluating ecological effects of present-day climatic change (Davis 1989*a*). Current rates of anthropogenic climate warming may be much faster than rates of climate change during the last 20 000 yr (Davis 1989*b*). Additionally, different species and systems have highly variable response times (e.g., beetles and tree species; see Graham and Grimm 1990), thereby limiting the usefulness of comparing community-wide changes that required millennia to those that occurred over decades. Finally, species interactions may be altered by changing climate, and thus may confound simple predictions of range shifts (Davis et al. 1998).

Predictions of biological responses to climate change have also been based on observations of communities perturbed recently by relatively strong climatological forces. The associations of ecological shifts such as marine range expansions (Lubchenco et al. 1993, Navarrete and Lubchenco 1993), coral bleaching (Glynn 1990), and fisheries declines (Ray et al. 1992) with episodic El Niño–Southern Oscillation (ENSO) events have been used as support for predictions of biological responses to climate change. Alternatively, extreme thermal gradients near power plant outfalls have been used as a proxy for climate change in community studies (Tissot et al. 1991, Tracy 1992). Even the use of these modern analogues remains speculative and is confounded by complex interactions (Lubchenco et al. 1993) that may or may not occur under present-day global climate change.

Several recent papers have documented community changes consistent with predicted responses to modern, multidecadal climate warming. Barry et al. (1995) compared two surveys conducted at the same intertidal site 60 yr apart, documenting a general increase in southern invertebrate species and a decrease in northern species. This faunal change was concomitant with an increase in yearly mean shoreline ocean temperatures. Roemmich and McGowan (1995*a*, *b*) used California Cooperative Oceanic Fisheries Investigations (CalCOFI) data from Southern California to illustrate a 70% decline in zooplankton since 1951, concurrent with sea surface warming of up to 1.5°C. CalCOFI data have also been used to document population increases and northward range expansion of sardine populations during multidecadal ocean warming since the mid-1970s (Lluch-Belda et al. 1992). Northward shifts in the spawning range of other pelagic fishes have also been associated with multidecadal climate shifts in the northeastern Pacific (Lluch-Belda et al. 1992, McGowan et al. 1996). Perhaps the clearest direct evidence of biotic responses to climate shifts is evident in time series data of marine organisms and sea temperature from the English Channel (Southward 1967, Southward et al. 1995). Southward found that warm-water species increased in abundance and cold-water species declined during periods of ocean warming (1920–1960; 1981–1995), whereas the opposite occurred during a cooling period (1960–1981). Parmesan's (1996) extensive surveys of Edith's checkerspot butterfly in western North America indicate that its range has shifted northward and toward higher elevation with climate warming. Holbrook et al. (1997) found an overall decline in abundance and shift toward dominance of southern reef fish species in the Southern California Bight following a shift to warmer ocean temperatures in the mid-1970s.

Here, we present a detailed examination of climate-related changes in the structure of the intertidal invertebrate community at Hopkins Marine Station (HMS) partially summarized by Barry et al. (1995). We consider changes in environmental parameters and the abundance of invertebrate species, over decadal (1931–1933 vs. 1993–1995) and interannual (1993 vs.1996) scales, along an intertidal transect first surveyed from 1931 to 1933 by W. G. Hewatt (Hewatt 1934, 1937). This expanded data set supports our earlier conclusions about the relationship between changes in invertebrate abundances and an increase in nearshore sea temperatures, and suggests that some species' ranges may be shifting northward. We evaluate several alternative hypotheses to explain these faunal changes using our expanded data set, historical records, and related studies. The most important alternative hypotheses considered are as follows.

Community shifts are due to short-term population variations.—Due to the limited sample size of two observations in 60 yr, observed trends in community structure may arise from random variation in species abundances, particularly if the invertebrate community varies greatly (i.e., seasonal or interannual variability) within the observation period. We address this alternative through the addition of a short-term (3-yr) comparison of invertebrate abundances along the transect.

Taxonomic or life history status controls community shifts.—Disproportionate changes in species' abundances of a particular taxon or life history trait would suggest that factors other than climate change were primarily responsible for the observed changes. For example, consistent changes in abundance of species having life histories including long-range planktonic dispersal may be suggestive of shifts in physical transport processes.

Community shifts are due to changes in intertidal habitat characteristics.—Because intertidal organisms inhabit the substratum or depend directly on benthic organisms for food, shelter, or living space, any changes in substratum characteristics through erosion or seismic activity would profoundly affect their abundance and distribution.

Vertical shifts in intertidal distributions confound interpretation of geographic range shifts.—Due to limited spatial sampling along the transect, changes in

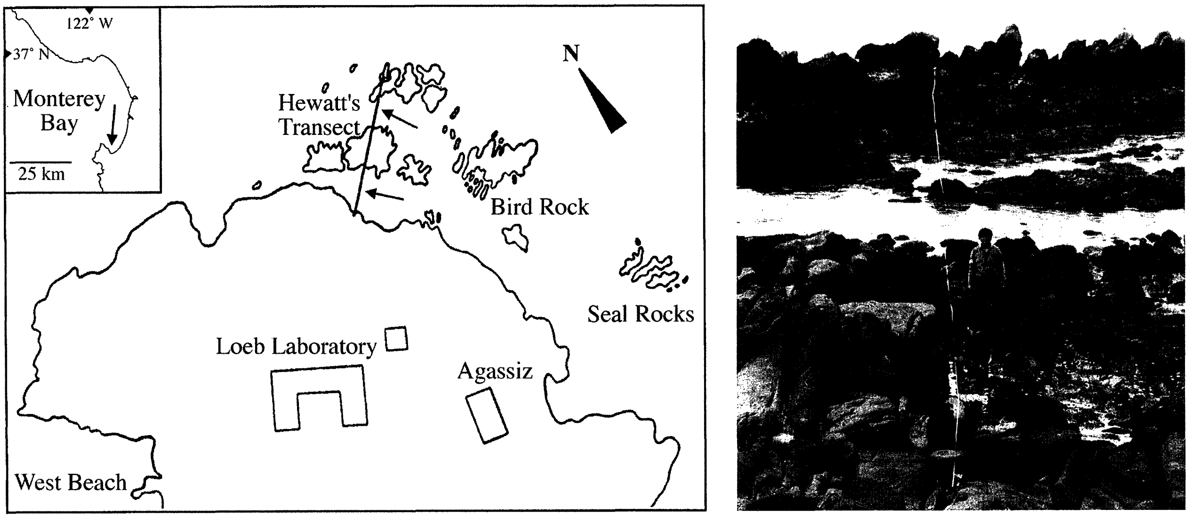

FIG. 1. (Left) Map of Cabrillo Point, California, USA (adapted from Hewatt 1937), showing the location of Hewatt's transect as well as prominent natural landmarks and Hopkins Marine Station buildings. For scale, the transect line is ~100 m long. Hewatt divided the transect into 108 square-yard plots, with plot 1 closest to shore. The locations of bolts used to mark the transect at the shoreward edges of plots 16 and 80 are indicated by arrows. Inset: the arrow points to the location of Cabrillo Point in southern Monterey Bay. (Right) R. D. Sagarin alongside Hewatt's transect. The eastern edge of the transect is marked by a white tape that connects bolts at the shoreward edges of plot 16 and plot 80 (indicated by arrows on the map). Tidal height at the time of the photo is ~0.24 m below Mean Lower Low Water. The photograph was taken 25 February 1998 by C. H. Baxter.

vertical distribution of species may appear as changes in abundance or changes in presence/absence of species along the transect, thereby influencing our interpretation of community changes.

Anthropogenic environmental changes have resulted in invertebrate community shifts.—Human impacts on the intertidal fauna at HMS may have come from pollution, exploitation of natural resources, or indirectly due to protection of harbor seals. These effects are explored largely through historical records.

Patterns of community changes have arisen from indirect species interactions.—It is unlikely that the significant changes observed in the abundances of 46 invertebrate species all reflect direct responses to any single variable. Many species may have responded indirectly to climate as a result of direct environmental control on their predators, competitors, symbionts, or other species that influence habitat quality (i.e., foliose algal cover). For example, two predators of intertidal invertebrates, the sea otter and Black Oystercatcher, returned to HMS in the years between Hewatt's study and ours. Their direct impacts on intertidal prey species will probably have cascading, indirect consequences to non-prey intertidal species. Changes in algal cover or composition in response to physical factors could also have far-reaching indirect effects on invertebrate abundances because many intertidal invertebrates depend on algae for food, primary habitat, or shelter from desiccation and predation.

ENSO-related events caused the observed community shifts.—El Niño–Southern Oscillation events are often manifest along the central California coast as increased northward oceanic transport and positive sea surface temperature anomalies, which may favor southern species and inhibit northern species. These potential effects may have influenced the intertidal community at HMS prior to our observation period, especially if ENSO events have become more intense and/or more frequent in the time interval between Hewatt's study and ours.

Community shifts are related to changes in upwelling intensity.—The study area is located within a prominent zone of coastal upwelling where cold, nutrient-rich water is brought to the surface by seasonal winds. Changes in upwelling patterns over the last 60 yr may have impacted the faunal composition at HMS through nutrient-driven changes in algal productivity, changes in settlement patterns of larvae, or alterations of biotic interactions.

METHODS

Study site

Our surveys were conducted in the exact location of an intertidal transect established by W. G. Hewatt in 1931 (Hewatt 1934, 1937). Hewatt's transect is located on a rocky outcrop known as Cabrillo Point (also: Point Almeja, China Point, Mussel Point) at HMS in Monterey Bay, California, United States (36°37.3′ N, 121°54.3′ W). The 98.8 m long transect is oriented roughly perpendicular to shore (bearing N 38° E) from high to low intertidal zones (Fig. 1, left). Hewatt (1937) published a detailed map, including height and substratum features, of the 108 contiguous square-yard (0.84-m^2) plots that make up the transect. Its coarse and granitic substratum includes two shallow subtidal channels, and a partially exposed granitic reef bordering the seaward edge shelters the transect from ocean swells.

The subtidal and intertidal area surrounding Hewatt's transect have been formally protected from collecting and disturbance as part of the state-designated Hopkins Marine Life Refuge since 1931. Fishing has been banned in the Refuge since 1984. A manager must approve any scientific experiments and collecting that occur in the Refuge.

Survey methods

Hewatt's transect was relocated with the aid of two of Hewatt's four original brass bolts that marked the transect (we have since permanently installed four 0.5 inch (~1.27 cm) diameter titanium plugs to mark the eastern edge of the transect). Changes in the invertebrate community on Hewatt's transect were quantified by comparing counts of invertebrates within a set of intertidal plots first surveyed by Hewatt between 1931 and 1933 (more precise dates of sampling are not available) with counts from the identical set of plots resampled between 1993 and 1996. We relocated the exact position of individual transect plots sampled by Hewatt, counting all invertebrates within the plots using methods described by Hewatt (1934), with any exceptions noted. All counts were performed during low tides by R. D. Sagarin and S. E. Gilman. In total, 57 plots were resurveyed between spring 1993 and late summer 1995 (Table 1). Data from these plots were used to analyze the various alternative hypotheses. During summer 1996, we resurveyed the first 19 plots that we surveyed in spring 1993 to assess short-term (3-yr) changes in species' abundances. The 19 plots were chosen for the short-term study because they were the only plots surveyed ≥3 yr prior to the resurvey in summer 1996. In terms of species composition and pattern of species' abundance changes, they were representative of the larger set of 57 plots (see *Results*). Additionally, these 19 plots included two plots (numbers 24 and 35) that Hewatt considered to be representative of the transect as a whole between 0 and 1.5 m tidal height.

During sampling sessions, a line was attached to the bolts to delineate the transect (Fig. 1, right). Individual plots were located precisely by measuring their known distance from either of Hewatt's bolts and, in most cases, matching features of the substratum with drawings from Hewatt's dissertation (Hewatt 1934). One edge of a 0.84-m^2 (1 square-yard) PVC quadrat was aligned with the transect tape and was held horizontally over the substratum of the study plot. The corners of the plot on the irregular rock surface were marked by dropping plumb lines from the quadrat corners, and the entire plot was defined on the substratum by connecting the marked corners with flexible brass chains.

Counts were performed as nondestructively as possible, although some animals were removed temporarily to aid counting or identification of species. With few exceptions, all individuals within a plot were counted, including those on or under marine plants or other species. Individuals with more than half of their body within a plot were judged as being in the plot (with the exception of large individual anemones *Anthopleura elegantissima* and *A. xanthogrammica,* which were counted in quarter-individual units). Because of the large surface area of a plot relative to its perimeter, counting errors due to edge effects were expected to be minimal (Krebs 1989).

Several species were ignored deliberately. Species that could not be readily and nondestructively identified using regional guides such as *Intertidal Invertebrates of California* (Morris et al. 1980) and *Light's Manual* (Smith and Carlton 1975) were not counted. Only species that could be readily enumerated with the unaided eye were counted. Thus, small animals that live abundantly in holdfasts of turf algae, such as the bivalve clam *Lasea cistula* and the gastropod snails *Barleeia* sp., *Caecum* sp., and *Tricolia* sp., were ignored. No such species were included in Hewatt's study, despite the presence of turf algae in Hewatt's photographs, and thus we assume that he also ignored them. Finally, although they inhabit transect plots, colonial organisms such as tunicates and sponges were not recorded, except those countable in discrete units (e.g., tunicates *Clavelina huntsmani* and *Polyclinum planum*). Although Hewatt mentioned in the text that colonial tunicates and sponges were generally common in some plots, he recorded in his tables only species that he claimed were the most common (the tunicate *Aplidium californicum* and the sponge *Lissodendoryx firma*), suggesting that he ignored less common colonial organisms.

All species except the barnacles *Balanus glandula* and *Chthamalus* sp. were counted directly. Where abundant, these barnacles were subsampled using 25 haphazard throws of a small quadrat within the larger study plot. Sizes for quadrats used to subsample barnacle species were determined based on Wiegert's method of minimizing relative variability and relative cost of sampling (Krebs 1989). Sizes were determined to be 2 × 2 cm and 3 × 3 cm for *Balanus* and *Chthamalus,* respectively. Considering the high densities of barnacles reported by Hewatt, he very likely estimated barnacle abundance, although no such method is reported.

Although Hewatt did not quantify algal cover, he provided qualitative accounts and photographs indicating a nearly 100% cover of *Pelvetia compressa* (=*Pelvetia fastigiata*) along sections of the transect. Hewatt provided little mention of other algae. Percentage cover of *Pelvetia* was estimated from 18 plots on the transect in July 1996, within a section reported

Table 1. Plots first surveyed by Hewatt in 1931–1933 and resurveyed by us for the present study (SBGB) along Hewatt's transect.

Plot	Height (m)	Zone	Hewatt	SBGB† 1993	SBGB† 1994	SBGB† 1995	SBGB† 1996	Plot	Height	Zone	Hewatt	SBGB† 1993	SBGB† 1994	SBGB† 1995	SBGB† 1996
1–10	2.38	high	x			x		60		low	x				
11	1.82	high	x			x		61	−0.20	low	x			x	
12	1.60	high	x			x		62	−0.09	low	x	x			x
13	1.60	high	x			x		63	0.04	mid	x	x			x
14	1.65	high	x			x		64	0.13	mid	x	x			x
15	1.43	high	x			x		65	0.17	mid	x	x			x
16	1.14	high	x		x			66	0.04	mid	x	x			x
17	0.87	mid	x		x			67	0.17	mid	x	x			x
18	1.06	mid	x		x			68	0.12	mid	x	x			
19	1.17	high	x		x			69	−0.04	low	x		x		
20	0.97	mid	x		x			70	−0.23	low	x		x		
21	1.00	mid	x		x			71	−0.01	low	x		x		
22	1.02	mid	x		x			72	0.31	mid	x		x		
23	1.05	mid	x		x			73	0.38	mid	x		x		
24	0.86	mid	x		x			74		mid	x				
25	0.93	mid	x		x			75		mid	x				
26	0.82	mid	x		x			76		mid	x				
27	0.88	mid	x	x			x	77		mid	x				
28	0.74	mid	x	x			x	78		mid	x				
29	0.74	mid	x	x			x	79		mid	x				
30	0.61	mid	x	x			x	80		low	x				
31	0.57	mid	x	x			x	81		low	x				
32	0.44	mid	x	x			x	82		low	x				
33	0.44	mid	x	x			x	83		low	x				
34	0.32	mid	x	x			x	84		low	x				
35	0.29	mid	x	x			x	85		low	x				
36	0.19	mid	x	x			x	86		low					
37	0.07	mid	x	x			x	87		low					
38	−0.08	low	x	x			x	88		low					
39	−0.20	low	x			x		89		low					
40	−0.21	low	x			x		90		low	x				
41	−0.24	low	x			x		91		low	x				
42		low						92		low	x				
43		low						93		low	x				
44		low						94		low	x				
45		low						95		low	x				
46		low						96		mid	x				
47		low						97		mid	x				
48		low	x					98		mid	x				
49	−0.16	low	x			x		99		mid	x				
50	−0.10	low	x			x		100		mid	x				
51	−0.12	low	x			x		101		mid					
52		low	x					102		mid					
53		low	x					103		mid					
54		low	x					104		mid					
55		low	x					105		low	x				
56		low	x					106		low					
57		low	x					107		low					
58		low	x					108		low					
59		low	x												

Notes: Hewatt pooled plots 1–10; average height is given. Tidal heights are given in meters relative to MLLW. Zones for plots in which tidal height was not directly measured were determined by position of plot relative to measured plots.

† Plot surveys from 1993–1995 were used for long-term comparison; 1996 surveys were for short-term comparison.

by Hewatt to incorporate a dense band of *Pelvetia.* We used visual estimates rather than random-point-quadrat (RPQ) methods, owing to their relative ease and comparable accuracy to RPQ (Dethier et al. 1993).

Elevations of the highest, lowest, and subjectively defined middle of each of the plots relative to mean lower low water (MLLW) were measured using a surveyor's transit and stadia rod. The average of these three measures was then used to classify each plot as "low" (<0.0 m relative to MLLW), "mid" (0.0–1.1 m above MLLW), or "high" (>1.1 m above MLLW; Table 1). Measurements were made relative to the second bolt on Hewatt's transect, reported by Hewatt to be 1.16 m above MLLW.

The height reported by Hewatt for the second transect bolt was checked for accuracy relative to a United States Coast and Geodetic Survey benchmark ("Mussel 1," 5.31 m above MLLW) located on a supratidal bluff at HMS, 38 m to the northwest of the second transect bolt. Additionally, MLLW was determined independently of Hewatt's bolts and other benchmarks in July 1994 in order to check the current height of Hewatt's bolt relative to sea level.

Analysis of biological data

Professional taxonomists confirmed species identifications in Hewatt's study. We updated his species assignments based on subsequent taxonomic revisions, using synonymies available in Smith and Carlton (1975) and Morris et al. (1980). In a few cases, taxonomic changes required lumping of recent species. For example, Hewatt (1934:55) reported high abundances of a "small growth form" of the limpet *Lottia digitalis* most likely to be *L. paradigitalis,* which was not described until 1960 (Fritchman 1960). To facilitate comparisons to Hewatt's counts of *L. digitalis,* we have combined our counts of *L. digitalis* and *L. paradigitalis.* Abundances of the southern snail *Acanthina punctulata* in the 1990s' surveys were compared to those of *A. spirata* (also southern) in Hewatt's survey. The two species were formerly united as *A. spirata,* and early records of *A. spirata* in Monterey Bay probably refer to *A. punctulata* (Morris et al. 1980).

Presence or absence of species was compared between surveys. Numbers of local additions (species present only in the later study) and deletions (present only in the former study) were compared for all species.

Several species were eliminated from further quantitative analyses under any of the following guidelines: (1) lack of quantitative data in either study (hermit crabs, for example, were only recorded as abundant, common, or rare by Hewatt, making quantitative comparisons impossible); (2) cases in which taxonomic ambiguities would confound our analysis of range-related changes (for example, we could not differentiate between a northern and southern species of *Chthamalus* barnacles); (3) a total of <10 individuals of a species present in both studies combined; or (4) a species that occurred in fewer than five separate plots in both studies. These restrictions were employed solely to facilitate quantitative comparisons and do not indicate a lesser importance of these species to the intertidal community along the transect.

Changes in abundance for all remaining species were evaluated with a paired t test using log-transformed abundances (Sokal and Rohlf 1995). Because the plots are precisely the same in Hewatt's study as in ours, counts for animals in each plot represent "before and after" treatments, which are typically tested with paired comparisons (Sokal and Rohlf 1995). For each species tested, the sample was the set of calculated differences in abundance between paired plots (i.e., for the 57 plots compared, $n = 57$). The null hypothesis states that the mean of these differences is zero. For the long-term comparison, significance was evaluated at the $\alpha = 0.05$ level. A Dunn-Sidak correction (Sokal and Rohlf 1995) was used to adjust the alpha level to correct for repeated comparisons of the 19 plots surveyed in 1931–1933, 1993, and 1996.

Potential latitudinal shifts in species' distributions were assessed by evaluating the overall pattern of change in species' abundances within geographic range groups. Species were divided by range categories based on published records of northern and southern range boundaries relative to the study area in Monterey Bay (primarily Brusca 1980, Morris et al. 1980, Ricketts et al. 1985). Species with a northern limit south of Cape Mendocino, California were considered "southern" species. Those with a southern limit north of Point Conception, California were considered "northern" species, and those with boundaries extending beyond these points in both directions were considered "cosmopolitan" species. Because few comprehensive records of species' ranges were available from the 1930s, our assignments to geographic range groups were based on relatively recent literature. Therefore, our evaluation of shifts in species' geographic ranges is somewhat conservative, owing to the potential for range shifts subsequent to Hewatt's studies, but prior to publications used for range assignments (e.g., migration of southern species north of Point Conception after 1933, but before Morris et al. 1980).

Changes in abundance among groups differing in dispersal ability were compared using a log-likelihood test. Information from Morris et al. (1980) and Strathmann (1987) was used to assign species to categories of dispersal ability, based on reproductive mode and planktonic duration.

Measurements of tidal elevation were used to look for changes in the vertical distribution of species between sampling surveys. Shifts in tidal elevation were analyzed in four ways. (1) Changes in species' abundances among tidal height categories were compared between surveys. (2) Distributions of cumulative percentage abundance vs. tidal elevation (in 15 elevation bins) were compared among surveys using a Kolmogornov-Smirnov test (Zar 1984). (3) Plots of cumulative distributions for each species were compared between Hewatt's and the present surveys to determine the direction of tidal height shifts. (4) An average tidal height for each species was calculated, based on abundance of the species in each plot weighted by the tidal height of each plot. Potential shifts in average tidal heights between surveys were evaluated for each species using Welch's approximate t test (Zar 1984).

Physical factors

Changes in nearshore ocean temperature over much of the 20th century were evaluated using daily records of shoreline sea temperatures measured at HMS for the period 1920–1995 (these data are compiled by Scripps Institute of Oceanography and are available online on the World Wide Web at ftp://nemo.ucsd.edu/pub/shore/past_years/). Linear least squares regressions were conducted on the annual mean, maximum, and minimum temperatures from this series to assess long-term trends. In addition, monthly means for the 13-yr periods preceding each study were plotted to compare in greater detail the temperature regimes leading up to and including the study periods. Thirteen-year periods were chosen to include the temperature signal of very strong El Niño events that occurred before each study.

Data series of ocean temperature at HMS were also divided into periods corresponding to three other studies detailing multidecadal warm and cool regimes in this century (Jones et al. 1991, U.S. Globec 1994, Southward et al. 1995). Regressions of temperature change and average maximum, minimum, and mean temperatures for each period were calculated to compare trends in the HMS record with the reported trends from these other sources.

Air temperature from four stations near Monterey Bay (Monterey, Santa Cruz, Watsonville, and Salinas) were compiled from Weather Bureau records for the period 1920–1948, and from the National Climatic Data Center for the period 1948 to the present. For all of the stations except the Monterey station (which was moved several times), there are nearly continuous records for these time periods. Temperature data from stations with continuous records were compared to discontinuous records from the Monterey station (least squares linear regression) to generate a continuous time series of predicted air temperatures for Monterey.

RESULTS

We counted 125 590 individual animals in 57 transect plots resurveyed between 1993 and 1995. Hewatt, by contrast, counted 64 741 individuals in these same plots (the large discrepancy in raw numbers of individuals counted is due mostly to 59 509 *Chthamalus* sp. barnacles recorded in the current survey, but not in Hewatt's). Sufficient data were gathered to compare abundances of 62 species quantitatively (Table 2). Seventy-three additional species were counted but eliminated from further analysis based on the defined protocol (Table 3).

Long-term study

Comparison of the abundances of animals in 57 plots over a long time scale (1931–1933 vs. 1993–1995) reveals a striking pattern of range-related change. Forty-six of 62 species showed a significant change in abundance ($P < 0.05$; Table 2). Of these, most southern species increased (10 of 11 species), most northern species decreased (5 of 7 species), and cosmopolitan species showed a weak trend toward decreases (12 species increased, 16 decreased; Fig. 2). The hypothesis that patterns of change in abundance were independent of range category was rejected using a log-likelihood test ($G = 10.4$, $P < 0.006$).

Short-term study

Nineteen of the 57 resurveyed plots were sampled again in 1996 to contrast community changes over a short period with those occurring over six decades. The dramatic shift in community structure over six decades (1996 or 1993 vs. Hewatt) in these 19 plots (Fig. 3A and B) was not apparent over only 3 yr (1993 vs. 1996; Fig. 3C). Of 49 species compared quantitatively, only four species changed significantly over 3 yr, including two southern species (the snail *Pseudomelatoma torosa,* which increased, and the limpet *Fissurella volcano,* which decreased), and two cosmopolitan species (the snail *Homalopoma luridum,* which decreased, and the limpet *Lottia asmi,* which increased). No range-related pattern of changes in abundances is apparent in the short-term comparison.

In stark contrast, the long-term (60-yr) pattern of change in these 19 plots (Fig. 3A and B) is similar to the widespread range-related shifts in species' abundances evident in the larger sample of 57 plots (Fig. 2). Additionally, large shifts in the abundance of many species are apparent in this long-term comparison (Fig. 3A and B). For example, even though the small sample size ($n \leq 19$) limits the statistical inference from these comparisons, the abundance of 18 species changed significantly between Hewatt's study and 1996. Of these, seven southern species increased significantly in abundance, with few significant changes in species from other range groups (Fig. 3B). Qualitatively, the range-related pattern of change is very similar to the overall comparison of 57 plots (Fig. 2).

Because statistical inference from a sample of 57 plots is greater than that for 19 plots, all other analyses are based on the overall long-term comparison (1931–1933 vs. 1993–1995) of 57 plots.

Presence/absence changes

Changes in the presence and absence of species from the transect revealed a potential flaw in utilizing such measures to assess community change when rare species are included in the analysis. When all species found in Hewatt's study or the present study are analyzed solely on presence or absence in a survey, no range-related pattern of change emerges (Fig. 4A). Additions of species (those present in the later study but not in the earlier) occur in every range group (although with a slightly higher percentage in the southern species), and the percentage of deletions (species present in the earlier study but not the later) is almost identical among range groups.

However, analysis of presence or absence based on all species is misleading because rare species (defined as those with <10 individuals in both studies; see *Methods*) are more likely to show random additions or deletions along a transect due to undersampling. Of the rare species, 93% were present in one study, but not in the other, whereas among the common species, only 40% were unique to one study. When rare species were excluded from analysis of presence/absence changes (Fig. 4B), nearly half of the southern species appeared in the 57 plots surveyed between Hewatt's survey and

TABLE 2. Changes in 62 species used for quantitative comparisons between Hewatt and the present study (SBGB).

						Total abundance¶	
Species†	Common name	Range‡	Disp.§	Change	Sig.‖	Hewatt	SBGB
Anthozoans							
Anthopleura elegantissima	anemone	S	3	+	*	0	209.25
A. elegantissima—clonal	anemone	N	1	−	*	224	105
Anthopleura xanthogrammica	anemone	N	3	−	*	34	9
Corynactis californica	anemone	S	1	+	*	0	523
Bivalves							
Chama pellucida	mussel	C		−	*	33	0
Kellia laperousii	mussel	C	3	−	*	19	0
Mytilus californianus	mussel	C	2	−	*	269	53
Crustaceans							
Alpheus clamator	shrimp	S		−	*	52	1
Balanus glandula	barnacle	C	3	−		44 678	40 838
Cancer antennarius	crab	C	3	−		12	2
Cancer productus	crab	C	3	−	*	17	0
Hemigrapsus nudus	crab	C	3	−		10	0
Pachycheles rudis	crab	C	3	−	*	377	1
Pachygrapsus crassipes	crab	C	3	−		102	74
Petrolisthes cinctipes	crab	N	3	−	*	174	0
Pugettia producta	crab	C	3	−		76	22
Tetraclita rubescens	barnacle	S	3	+	*	67	2 592
Echinoderms							
Amphipolis pugetana	brittle star	C	3	−	*	114	0
Asterina miniata	sea star	C		+		4	37
Leptasterias hexactis	sea star	N	1	−	*	223	26
Lissothuria nutriens	sea cucumber	S		−		25	0
Pisaster ochraceus	sea star	C	3	−	*	106	1
Strongylocentrotus purpuratus	urchin	C	3	−	*	527	51
Gastropods							
Acanthina punctulata	snail	S	3	+	*	61	122
Acmaea mitra	limpet	C		−	*	39	1
Alia carinata	snail	C		−	*	4 379	255
Amphissa versicolor	snail	S	3	−		506	291
Bittium eschrichtia	snail	C	1	+	*	0	132
Calliostoma ligatum	snail	N	2	+	*	55	142
'Collisella' scabra	limpet	C	3	+	*	187	689
Crepidula adunca	snail	N	1	+	*	353	811
Erato vitellina†	snail	S	3	+	*	0	13
Fissurella volcano	keyhole limpet	S		+	*	24	59
Hermissenda crassicornis	sea slug	C	3	−		10	7
Hipponix cranioides	hoof snail	C	1	−	*	22	0
Homalopoma luridum†	snail	C		+	*	0	199
Hopkinsia rosacea	sea slug	C		−	*	33	0
Lacuna marmorata†	snail	C	3	+	*	0	189
Littorina keenae	snail	C	3	+	*	466	1 604
Littorina scutulata/plena	limpet	C	3	+	*	3 960	4 742
Lottia asmi†	limpet	C		+	*	0	25
Lottia digitalis	limpet	C	3	−		605	156
Lottia limatula	limpet	C		−		478	263
Lottia pelta	limpet	C		+	*	28	41
Ocenebra circumtexta†	snail	S		+	*	0	45
Ocenebra lurida	snail	C		−	*	110	0
Pseudomelatoma torosa	snail	S		+	*	0	23
Rostanga pulchra	sea slug	C	3	−	*	12	0
Serpulorbis squamigerus†	snail	S		+	*	0	872
Tectura paleacea†	limpet	C		+	*	0	49
Tectura scutum	limpet	N	3	−	*	825	22
Tegula brunnea	snail	C		+	*	173	1 910
Tegula funebralis	snail	C	2	+	*	3 673	6 447
Tegula pulligo	snail	C	2	+		0	23
Polychaetes							
Arabella iricolor†	segmented worm	C		+	*	0	14
Halosydna insignis	segmented worm	C		−	*	192	0

TABLE 2. Extended.

Density (no./m^2)#			
Hewatt		SBGB	
Mean	1 SD	Mean	1 SD
0.00		4.37	4.54
4.68	16.75	2.19	25.29
0.71	2.02	0.19	0.91
0.00		10.92	45.40
0.69	4.79	0.00	
0.40	1.48	0.00	
5.62	13.30	1.11	8.43
1.09	7.39	0.02	0.14
933.12	4 187.27	852.92	4 254.74
0.25	1.11	0.04	0.58
0.36	0.75	0.00	
0.21	2.31	0.00	
7.87	36.75	0.02	0.45
2.13	5.25	1.55	2.41
3.63	14.78	0.00	
1.59	6.27	0.46	1.26
1.40	9.34	54.14	276.05
2.38	8.75	0.00	
0.08	1.10	0.77	2.75
4.66	13.04	0.54	1.67
0.52	4.79	0.00	
2.21	7.53	0.02	0.45
11.01	23.70	1.07	4.30
1.27	4.52	2.55	4.79
0.81	3.27	0.02	0.58
91.46	141.24	5.33	11.97
10.57	20.34	6.08	11.02
0.00		2.76	7.57
1.15	5.00	2.97	7.25
3.91	12.53	14.39	43.10
7.37	14.81	16.94	19.07
0.00		0.27	1.57
0.50	2.48	1.23	1.93
0.21	1.91	0.15	1.14
0.46	1.73	0.00	
0.00		4.16	14.03
0.69	1.57	0.00	
0.00		3.95	9.35
9.73	46.77	33.50	355.30
82.71	252.79	99.04	180.89
0.00		0.52	1.98
12.64	83.51	3.26	2.98
9.98	22.48	5.49	9.89
0.58	4.72	0.86	1.68
0.00		0.94	1.73
2.30	7.89	0.00	
0.00		0.48	2.00
0.25	1.10	0.00	
0.00		18.21	49.72
0.00		1.02	5.63
17.23	78.42	0.46	2.85
3.61	14.32	39.89	59.83
76.71	136.45	134.65	164.55
0.00		0.48	12.42
0.00		0.29	2.66
4.01	11.67	0.00	

ours. A few northern species observed by Hewatt disappeared from the plots during this period and no new northern species were added. Cosmopolitan species were added and deleted in similar numbers. Although this pattern is not as strongly defined as the pattern of abundance changes, it nonetheless supports the range-related nature of community changes at HMS.

Changes by taxonomic grouping

The pattern of change in species' abundances varied among higher taxa (Table 2). Four of 10 crustacean species decreased in abundance, and only one increased in abundance between surveys. One southern species (the barnacle *Tetraclita rubescens*) increased, whereas one (the shrimp *Alpheus clamator*) decreased. One northern species (the crab *Petrolisthes cinctipes*) and two cosmopolitan species (the crabs *Cancer productus* and *Pachycheles rudis*) decreased.

Gastropod mollusk abundances changed markedly over 60 yr. Of 34 gastropod species compared quantitatively, 26 changed in abundance, with 19 species increasing. Despite a general increase in the abundance of gastropods, changes in this group enhance the overall pattern of range-related changes. Of the gastropods that changed, all six southern species increased in abundance. Eleven cosmopolitan species increased, whereas six decreased. One of three northern species decreased in abundance, whereas two increased. One species that increased (the slipper snail *Crepidula adunca*) is a symbiont on the turban snail *Tegula* sp., which also increased in abundance, and the ratio of *Crepidula* to *Tegula* remained unchanged (paired t test, $P = 0.584$).

Anemones encountered along the transect showed the characteristic response, with southern species increasing and northern species decreasing in abundance. Two southern anemones, the clonal *Corynactis californica* and the solitary form of *Anthopleura elegantissima,* each increased in abundance. The clonal form of *A. elegantissima* and the solitary anemone *A. xanthogrammica,* both northern species, decreased.

Changes by dispersal ability

Changes in the abundances of species were unrelated to dispersal ability as estimated by mode of development. Sufficient information concerning natural history was available to assign 42 species (of 62 species that were compared quantitatively) to categories based on their dispersal ability (Table 2). Species in all categories of dispersal ability had similar patterns of change, with no significant differences between numbers of species that increased, decreased, or did not change (Table 4). A log-likelihood test (dispersal group × direction of change) was nonsignificant ($G = 2.13$, $P > 0.71$), rejecting the hypothesis that the direction of change was dependent of dispersal ability.

Changes in habitat characteristics

We found no evidence, as observed in other intertidal systems (Bodin and Klinger 1986, Castilla 1988, Cas-

TABLE 2. Continued.

Species†	Common name	Range‡	Disp.§	Change	Sig.‖	Total abundance¶	
						Hewatt	SBGB
Polyplacophorans							
Lepidochitona hartwegii	chiton	S	2	+	*	24	90
Mopalia muscosa	chiton	C	2	−		24	17
Tonicella lineata	chiton	N	3	−		33	8
Sipunculid							
Phascolosoma agassizii	peanut worm	C	3	−	*	441	6
Urochordates							
Clavelina huntsmani	tunicate	C	1	−		565	466
Polyclinum planum	tunicate	S	1	+		4	8

† Species were not listed by Hewatt.

‡ Range abbreviations: C, cosmopolitan; N, northern; and S, southern.

§ Dispersal categories: 1, brooder/short dispersal; 2, <10 d in plankton; 3, >10 d in plankton.

‖ Significant change in abundance, using paired *t* test; $*P < 0.05$.

¶ Total abundance is summed over 57 quadrats.

Densities are converted from average no. per square yard to average no. per square meter.

tilla and Oliva 1990), that subsidence or uplift of the substratum relative to sea level (especially due to seismic activity) has occurred at HMS during the 60 yr between our studies. We measured Hewatt's second bolt (reported by Hewatt to be at 1.16 m above MLLW) to be 1.165 m above MLLW (with MLLW determined independently in July 1994). We believe that the difference of 0.005 m from expected is due to measurement error, and not due to shifts in the tidal height of the transect. Additionally, the difference between a U.S. Coast and Geodetic Survey benchmark on shore (5.31 m above MLLW) and Hewatt's second bolt was 4.15 m, exactly as expected if there had been no subsidence or uplift of the intertidal area relative to the surrounding shore since Hewatt's study.

Vertical distribution shifts

Although abundances of many species changed within tidal height zones, we detected no directional trend (in tidal height distributions) among species (Table 5). Only minor differences in patterns of change within tidal zones were detected. Within high-zone plots, three species increased in abundance (paired *t* test, $P < 0.05$). Twenty-six species changed in abundance in the mid-zone plots, with 15 increasing and 11 decreasing. In the low zone, 29 species changed in abundance, with 14 increasing and 15 decreasing. A chi-square analysis ($P > 0.05$) suggested that no significant direction of change (species increasing or decreasing overall) occurred in any zone.

The cumulative tidal height distribution of 21 species differed between sampling periods (Kolmogornov-Smirnov test, $P < 0.05$). Analysis of direction of shift (examples in Fig. 5) for these 21 species revealed that four species shifted to lower intertidal positions, nine shifted higher in the intertidal, and eight shifted higher in part of their vertical range and lower in other parts.

Average tidal heights changed for only four species (the sea slug *Hermissenda crassicornis,* the mussel *Mytilus californianus,* the crab *Pachygrapsus crassipes,* and the limpet *Tectura scutum*). Each also showed significantly different cumulative distributions between surveys. Of these, only *M. californianus* and *T. scutum* changed in abundance (both decreased) between Hewatt's study and the present (Table 6). No geographic range-related patterns were apparent from these height shifts.

Changes in algal cover

Hewatt's photographs and descriptions report a dense band of the brown alga *Pelvetia compressa* between the 0.61- and 1.07-m tidal level, with 100% cover reported up to 0.91 m. *P. compressa* was uncommon and patchy along the transect during our investigation of Hewatt's transect. The maximum percentage cover in any plot on the transect was 30%, and most plots within and surrounding Hewatt's reported *Pelvetia* zone were entirely devoid of this alga (Table 7). No other fucoid algae were observed along the transect. Other turf algae (e.g., *Endocladia muricata* and *Chondracanthus canaliculatus*) are common in the transect, with up to 100% cover in some plots, but their abundances were not quantified.

Ocean temperature

Yearly average mean, maximum, and minimum shoreline temperatures increased significantly during the period 1920–1995 (Fig. 6A). Linear regression coefficients for annual mean, maximum, and minimum shoreline temperatures for HMS vs. year were 0.012, 0.019, and 0.010, respectively ($P \ll 0.01$ in all cases), representing an increase of mean annual sea surface temperature of 0.79°C, 1.26°C and 0.66°C, respectively, between 1931 and 1995. Despite the apparent greater increase in maximum temperatures, tests for homogeneity of slopes between maximum and mean ($P =$

TABLE 2. Continued, Extended.

Density (no./m²)#			
Hewatt		SBGB	
Mean	1 SD	Mean	1 SD
0.50	2.94	1.88	5.34
0.50	2.73	0.36	0.99
0.69	8.20	0.17	0.53
9.21	34.20	0.13	3.46
11.80	83.37	9.73	46.44
0.08	0.00	0.17	3.37

0.17) and maximum and minimum ($P = 0.11$) temperatures were nonsignificant. Average conditions during the 13-yr period preceding our study were consistently warmer than the same period preceding Hewatt's study, with a difference in mean temperature of 0.99°C and a maximum difference in seasonal temperature of 1.94°C in late July (Fig. 6B).

Air temperature

Maximum air temperature increased slightly, although nonsignificantly, at Salinas and Watsonville, and decreased (nonsignificantly) at Santa Cruz over the period January 1929–May 1996. Minimum air temperature increased nonsignificantly at all stations. Because the Monterey recording station was relocated several times during this century, patterns of change in its temperature record were affected most by the microclimate of its locale. To estimate changes in air temperature at Monterey, we used a multiple regression of each other station on the Monterey time series to generate predicted air temperatures for Monterey (Fig. 7). Multiple regression coefficients for monthly minimum and monthly maximum temperatures were 0.985 and 0.993, respectively. The slopes of the predicted minimum and maximum Monterey air temperatures were positive, but nonsignificant (0.001 and 0.006, respectively; R^2 values of 0.0363 and 0.0009, respectively).

ENSO

El Niño–Southern Oscillation events of varying intensities occurred in the 13-yr periods preceding and during each study (Fig. 8). Quinn et al. (1987) provide the most consistent historical record to compare the magnitude and frequency of ENSO events. Six of 13 years preceding Hewatt's survey were classified as ENSO years, including a strong 2-yr event (1925–1926). Five of 13 years preceding our surveys were ENSO years, including the very strong event of 1982–1983, considered to be the strongest event of the century before our surveys (Hansen 1990). Both studies were conducted during ENSO years, including weak (1931), moderate (1994, 1995; Vernon Kousky, *personal communication*), and strong (1932) events. Some investigators consider the entire 1990–1995 period to be an ENSO event (Trenberth and Hoar 1996).

Although the 1958–1959 and 1982–1983 events (and possibly the 1940–1941 event, which occurred at the end of a gap in data collection) seem to co-occur with large positive spikes in nearshore ocean temperature, other major ENSO events were not concurrent with anomalous warm periods at HMS (Fig. 6A). ENSO events did not correspond with any periods of anomalous air temperature.

DISCUSSION

Range shifts or population changes?

The most compelling pattern of change in the invertebrate community at HMS between the 1990s and 1930s is linked to geographic ranges of species. Because these data were collected from a single location, it is difficult to determine if changes in species' abundances are indicative of a northward migration in faunal ranges, or simply local changes in abundance without any geographic shift. However, analysis of the range-related pattern of change among many species can be used to reject or support hypotheses concerning the direction (if any) of range migrations in response to factors (e.g., climate) expected to have widespread effects within the community.

If species' ranges have been shifting northward, several simple predictions should be met in observations from a single site. First, southern species should colonize sites north of their present range, whereas northern species should become locally extinct near their southern range boundary. Thus, there should be additions of southern species and deletions of northern species. Analysis of non-rare species for changes in presence or absence (Fig. 4B) supported this prediction, especially for southern species. Almost half of the southern species were local additions, whereas no northern species were added. Cosmopolitan species showed a mix of additions, deletions, and species present in both studies. Inclusion of all species obscured this pattern (Fig. 4A), largely due to changes in rare species, which are sampled poorly along the transect. Thus, even when presence/absence data are available (and often these are the only types of data available from historical records), they may not be appropriate for testing this prediction. Note that we were able to restrict our analysis to non-rare species only because abundance estimates were available for all species.

Second, the abundance of southern species should increase and the abundance of northern species should decrease. For species present in both studies, this prediction assumes that each species' abundance is higher toward the center of its geographic range. Several authors (e.g., Brown 1984, Enquist et al. 1995) have suggested that the abundance of a species along its range

TABLE 3. Species recorded, but eliminated from quantitative comparison.

Species	Common name	Reason§
Anthozoans		
Balanophyllia elegans†	cup coral	3
Epiactis prolifera	anemone	3
Bivalves		
Epilucina californica§	clam	3
Hinnites giganteus	scallop	3
Modiolus capax	mussel	3
Mytilus carpenteri†	mussel	3
Mytilus edulis†	mussel	3
Bryozoans		
Cryptosula pallasiana‡	bryozoan	1
Crustaceans		
Atylopsis sp.‡	amphipod	2
Betaeus harfordi	shrimp	4
Cancer jordani	crab	3
Caprella sp.	shrimp	3
Chthamalus sp.†	barnacle	2
Cirolana harfordi‡	isopod	1
Cryptolithodes sitchensis†	crab	3
Hapalogaster cavicauda	crab	3
Heptacarpus pictus	shrimp	1
Idotea urotoma‡	isopod	4
Ligia occidentialis‡	isopod	4
Lophopanopeus leucomanus leucomanus†	crab	3
Lophopanopeus leucomanus heathii	crab	4
Loxorhynchus crispatus†	crab	3
Megabalanus californicus	barnacle	4
Melita palmata‡	amphipod	1
Mimulus foliatus	crab	4
Pagurus sp.	hermit crab	1
Paraxanthias taylori	crab	3
Pollicipes polymerus	barnacle	3
Pugettia richii	kelp crab	4
Spirontocaris picta	shrimp	1
Echinoderms		
Amphiodia occidentalis	brittle star	4
Henricia leviuscula	sea star	3
Leptosynapta inhaerens‡	sea cucumber	3
Ophiactis simplex†	brittle star	3
Ophioderma panamense†	brittle star	3
Ophioplocus esmarki†	brittle star	3
Ophiothrix spiculata	brittle star	3
Pisaster giganteus†	sea star	3
Gastropods		
Amphissa columbiana†	snail	3
Anisodoris nobilis	sea slug	3
Calliostoma canaliculatum	snail	3
Ceratostoma foliatum†	snail	3
Coryphella trilineata†	sea slug	3
Cuthona lagunae†	sea slug	3
Dendronotus iris	sea slug	3
Doriopsilla albopunctata	sea slug	3
Epitonium tinctum†	snail	3
Fusinus luteopictus†	snail	3
Haliotis cracherodii	abalone	3
Laila cockerelli	sea slug	3
Lottia connus/pelta hybrid	limpet	3
L. ochracea	limpet	3
Megatebennus bimaculatus	keyhole limpet	3
Nassarius mendicus cooperi†	snail	3
Nucella emarginata	snail	3
Onchidella borealis†	limpet	3
Tegula montereyi†	snail	3
Nemerteans		
Emplectonema gracile†	ribbon worm	4
Paranemertes peregrina	ribbon worm	1
Platyhelminthes		
Alloioplana californica‡	flat worm	1
Polychaetes		
Glycera americana†	segmented worm	3
Lumbrinereis sp.‡	segmented worm	2
Nereis sp.‡	segmented worm	1
Spirorbis	segmented worm	1
Polyplacophorans		
Chaetopleura gemma†	chiton	3
Lepidozona mertensii	chiton	3
Nuttallina californica	chiton	3
Porifera		
Leucandra heathi‡	sponge	1
Plocamia karykina‡	sponge	1
Urochordates		
Aplidium californicum	tunicate	1
Archidistoma molle†	tunicate	1
Vertebrata		
Oligocottus maculosus	sculpin	3
Rimicola eigenmonnii†	cling fish	3

† Species not recorded by Hewatt in plots surveyed by both studies.

‡ Species deliberately not counted by us in plots surveyed by both studies.

§ Reason for elimination: 1, lack of quantitative data; 2, taxonomic ambiguities; 3, <10 individuals in both studies; 4, found in <5 quadrats in both studies.

is generally Gaussian, although some observations contradict this notion (e.g., Svensson 1992). However, as long as there is some tail in the distribution of abundance of the species (i.e., abundances at the edges of the range are generally lower than elsewhere in the range), this prediction is supported because the study site, by definition, is located in the edges of our southern and northern species' ranges. As a corollary, because the study site is located in the central portion of our cosmopolitan species' ranges, no trend in the direction of abundance changes in these species is expected. Our results strongly support these expectations. In the current study, northern species decreased in abundance, southern species increased, and cosmopolitan species showed no directional trend. This pattern was first noted by Barry et al. (1995) after examining 35 transect plots, and it appears more clearly in our larger survey of 57 plots.

Changes in the abundances of several species of intertidal and shallow subtidal organisms reported from

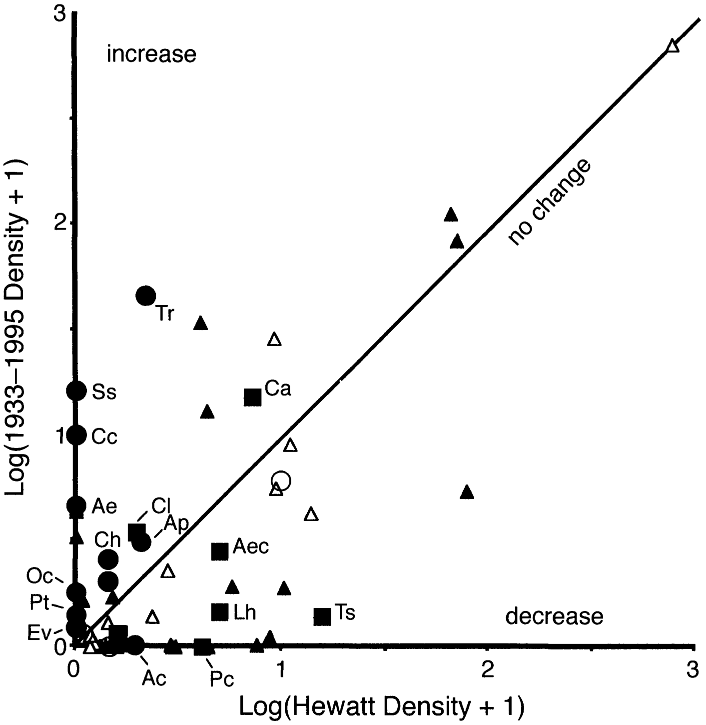

FIG. 2. Plot of density in 1995 vs. density in Hewatt's study for 62 species. Solid symbols are species that showed a significant change in abundance between the two studies (paired *t* test, $P < 0.05$): southern species, ●; northern species, ■; cosmopolitan species, ▲. Abbreviations are as follows: *Acanthina punctulata* (Ap), *Alpheus clamator* (Ac), *Anthopleura elegantissima* (Ae), *Anthopleura elegantissima* clonal form (Aec), *Anthopleura xanthogrammica* (Ax), *Calliostoma ligatum* (Cl), *Corynactis californica* (Cc), *Crepidula adunca* (Ca), *Lepidochitona* (=*Cyanoplax*) *hartwegii* (Ch), *Erato vitellina* (Ev), *Fissurella volcano* (Fv), *Leptasterias hexactis* (Lh), *Ocenebra circumtexta* (Oc), *Petrolisthes cinctipes* (Pc), *Pseudomelatoma torosa* (Pt), *Serpulorbis squamigerus* (Ss), *Tectura scutum* (Ts), and *Tetraclita rubescens* (Tr).

HMS and other central California sites are also consistent with the hypothesis of northward range migrations. Several of the species for which we have additional information will be discussed.

Serpulorbis squamigerus, a sessile vermetid gastropod now abundant at HMS and the central California coast, has changed dramatically in abundance at HMS over the last 60 yr. Hewatt (1934) did not report *S. squamigerus* on the transect or on his comprehensive list of species for HMS. Hadfield (1966) commented that, "Nowhere north of Pt. Conception have large numbers of *S. squamigerus* been seen, and on the Monterey Peninsula they are rare"; he relied on collections of *S. squamigerus* from southern California for his thesis work. As late as 1980, *S. squamigerus* was reported to have a range from Monterey Bay to Baja, with individuals occurring only singly or in small clusters of tubes in Monterey Bay (Morris et al. 1980). By May 1993, however, we counted abundances along Hewatt's transect to 273 *S. squamigerus*/m^2. Overall density of *S. squamigerus* increased significantly again from 1993 to 1996. Similarly high densities were also documented elsewhere in the intertidal at HMS during July 1996 (A. Sagarin, *unpublished data*). It is now common at intertidal sites in the Monterey region, and occurs in densities $>$2700/m^2 on protected rocks near the Coast Guard Wharf in Monterey.

Other evidence documents the northward expansion of *S. squamigerus* along the central California coast. Extensive monitoring of intertidal communities by John Pearse and collaborators from the University of California, Santa Cruz (UCSC) corroborate our observations. No *S. squamigerus* were observed by the UCSC group during surveys of 10 intertidal sites between Pigeon Point, California and Soquel Point (northern Monterey Bay) from 1971 to 1973. When the UCSC researchers resampled these sites in 1996, *S. squamigerus* was found at eight sites, with high abundances at four sites (J. Pearse, *unpublished data*). One author (R. D. Sagarin) found *S. squamigerus* as far north as Fitzgerald Marine Reserve, Half Moon Bay, California (37°31′ N) in January 1994 and June 1996, although it was absent from species lists compiled in 1987 by rangers at the Reserve. These findings indicate that *S. squamigerus* has successfully colonized areas northward of its known range in recent years.

The increased abundance of *Lepidochitona hartwegii* (=*Cyanoplax hartwegii*), a southern chiton with a published range from Monterey Bay to Baja (Morris et al. 1980), on Hewatt's transect is evident elsewhere at HMS and on the central California coast. A class at HMS measured the maximum density (they did not record average densities) of this species to be =30 chitons/m^2 under *Pelvetia* in 1974 (DeBevoise 1975). In July 1996, its density in 16 0.25-m^2 quadrats placed on *Pelvetia* at HMS was 45.8 ± 20.9 chitons/m^2 (mean ± 1 SD). The UCSC group also documented an increase in *L. hartwegii* in northern Monterey Bay and the open coast north of the bay (J. Pearse, *personal communication*).

Changes in the reported distribution and abundance of *Corynactis californica,* a southern corallimorph

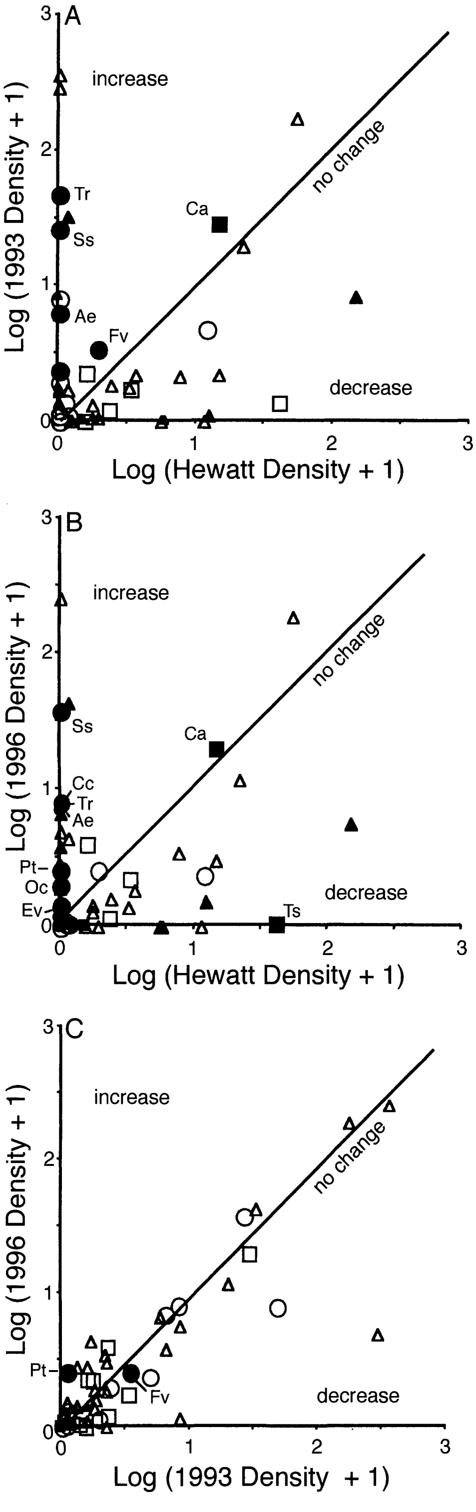

Fig. 3. Plot of densities of 61 species for the 19 plots surveyed in Hewatt's study, in 1993, and in 1996. Solid symbols are species that showed a significant change in abundance between the two studies (paired *t* test with Dunn-Sidak correction, $P < 0.025$). Symbols and abbreviations are as in Fig. 2. (A) 1993 vs. Hewatt's study. (B) 1996 vs. Hewatt's study. (C) 1996 vs. 1993.

anemone not encountered by Hewatt, but presently abundant in lower intertidal plots on the transect, also support our hypothesis of a northward expansion of its range over the last six decades. *C. californica* was assigned to the southern species group for this study because the most authoritative and timely reference on corallimorph anemones (Hand 1954) reported its northernmost limit near Salt Point (Sonoma County, California). At the time of Hewatt's study, this species was known only from Monterey Bay (Johnson and Snook 1927, Hand 1954). Moreover, Kozloff (1973, 1974) did not list *C. californica* for the Pacific Northwest. It appeared more recently in faunal guides to the Pacific Northwest in 1983 and 1993, where it was reported as "rarely encountered intertidally north of Oregon" (Kozloff 1983, 1993).

The solitary form of the anemone *Anthopleura elegantissima* is considered a southern species (Francis 1979), and has appeared in the transect and at HMS since Hewatt's study, generally replacing the more northern clonal form. It is clear from the high abundance of *A. elegantissima* per plot recorded by Hewatt, as well as from contemporary reports (Gislen 1943), that the clonal form existed at HMS in significant numbers in 1933, but the solitary form may have been rare or absent. In their 1947 investigation of HMS, Stephenson and Stephenson (1972) noted a solitary anemone, *Anthopleura artemisia,* which (based on their description) is more likely to have been the solitary form of *A. elegantissima.* R. Paine (*unpublished data*) also reported anemones that were most likely to be solitary *A. elegantissima* from Hewatt's transect during his investigation in late February 1983.

Other investigators noted evidence of northward migration of species into Monterey Bay consistent with predicted climate-related faunal shifts. *Kelletia kelletia,* a shallow subtidal whelk from southern California, was first reported in Monterey Bay in the late 1970s (Jim Watanabe, *personal communication*). A range extension published in 1981 (Herrlinger 1981) was based on five scattered individuals near HMS; by the summer of 1994, *K. kelletia* was measured in densities to 0.3 whelks/m^2 off HMS (Gary Villa and J. Watanabe, *personal communication*). In 1996, their numbers were considerably lower (0.04 whelks/m^2; R. D. Sagarin, *personal observation*). Anecdotal evidence suggests that the recent decrease may be due to otter predation, a more cryptic distribution beneath the sediment surface (predator avoidance behavior), or both (Gary Villa, *personal communication*).

In recent years, lobster (*Panulirus interruptus*) have been reported by divers off the Monterey Peninsula (C. Baxter, *unpublished data*). Other southern species (e.g., the frog shell *Bursa californica*) have been observed recently in Monterey waters by divers from the Monterey Bay Aquarium. Zimmerman et. al (1996) documented a massive decline of eel-grass beds near HMS following the 1993 appearance and rapid population

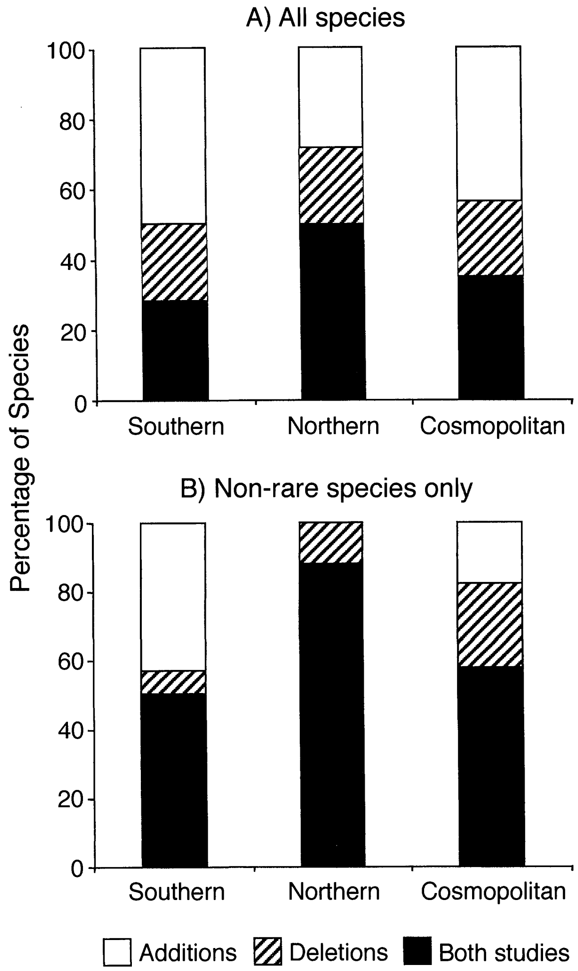

FIG. 4. (A) Changes in presence/absence of all species recorded either by Hewatt or by us (SBGB) in the 57 plots resurveyed between 1993 and 1995. "Additions" are species recorded by SBGB, but not Hewatt. "Deletions" are species recorded by Hewatt, but not SBGB. "Both studies" are species recorded by both Hewatt and SBGB. (B) Changes in presence/absence of non-rare species only (defined as those with >10 individuals recorded by either Hewatt or SBGB).

growth of the southern eel-grass limpet *Tectura depicta* (oval form), which had not been previously recorded from Monterey Bay.

Alternative hypotheses

Community shifts are due to short-term population variations.—An important result of this study is the rejection of the hypothesis that community changes over six decades may represent relatively short-term fluctuations in species abundances. Community changes observed in a subset of plots over three years were minor and unrelated to geographic ranges of species (Fig. 3C), compared to the widespread changes documented in these same plots over 60 years (Fig. 3A and B).

TABLE 4. Changes in abundances of species based on dispersal ability.

Category†	Increase	Decrease	Nonsignificant
Short	3	3	2
Medium	3	1	2
Long	7	11	10

† Short, no planktonic period; medium, <10 d in plankton; long, >10 d in plankton.

Seasonal fluctuations in species' abundances are unlikely to have contributed to the documented changes in the HMS invertebrate community. Because Hewatt did not report dates of sampling, any correspondence of our sampling dates or seasons with his survey is not known. Hewatt did segregate samples among seasons, but discounted the importance of seasonal variation along the transect, noting, "On account of the small changes in the number of specimens of the various species present during the different seasons, the results [of seasonal variation in abundance] were not considered significant enough to justify the inclusion of these seasonal data. The examples given in the tables for each zone [abundances recorded at one sampling period] illustrate the relative frequency of the species at all seasons" (Hewatt 1934:67). Glynn (1965) reported little seasonal variation in the species composition of the *Balanus–Endocladia* association at HMS. There appears, nonetheless, to be some seasonal variation in the substratum of the transect, with many smaller channels becoming filled with sand and shell debris during winter. This debris may bury small, sessile organisms such as anemones and tunicates, and may restrict movement or distribution of organisms that live on rock surfaces (chitons, snails, and limpets). Our surveys were conducted in summer and early fall when these channels are relatively free of debris.

Taxonomic or life history status controls community shifts.—It is notable that the range-related pattern of

TABLE 5. Changes in abundances of species within three tidal height zones.

Zone, range	Chi-square†	Increase	Decrease	Nonsignificant
High	0.09			
northern		0	0	3
southern		2	0	2
cosmopolitan		1	0	6
total		3	0	11
Mid	0.50			
northern		1	4	3
southern		6	0	4
cosmopolitan		8	7	11
total		15	11	18
Low	0.77			
northern		2	2	4
southern		6	2	1
cosmopolitan		6	11	10
total		14	15	15

† P values for H_0: increases or decreases in species abundances were not more common than expected in each zone. Significant increases or decreases were determined by paired t test ($P < 0.05$) for each species within each zone.

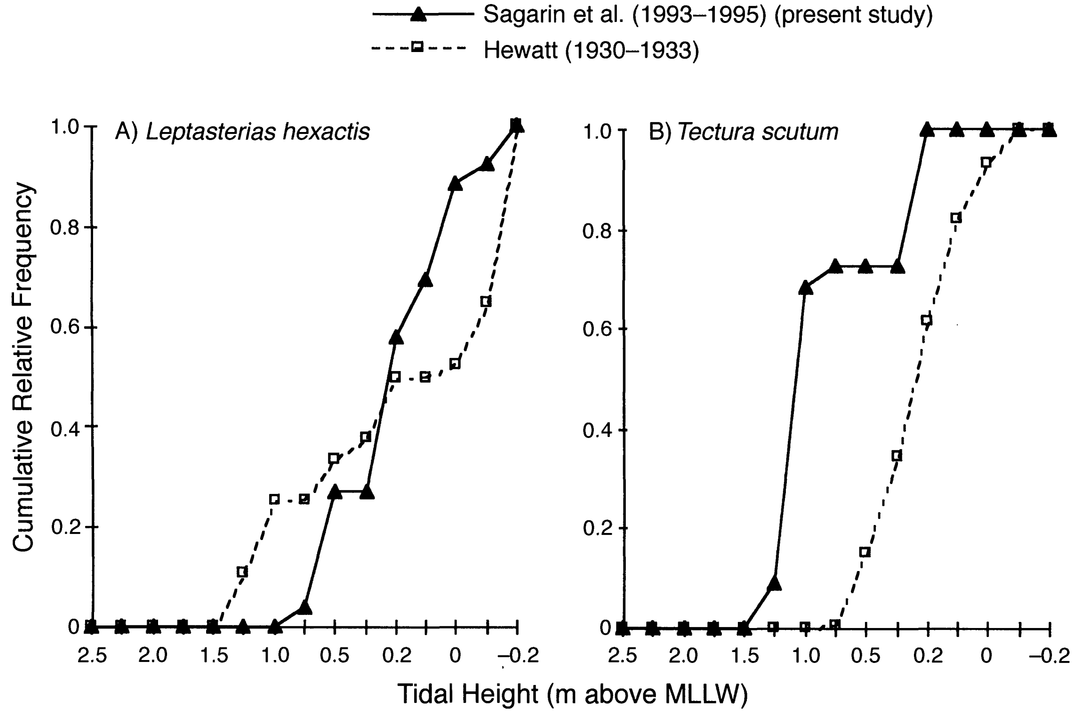

FIG. 5. Examples of cumulative tidal height distributions created for each species on the transect. A shift to the left between the two studies indicates a shift toward higher tidal heights. A shift to the right is toward lower tidal heights. Although the sea star *Leptasterias hexactis* (A) has a significantly different distribution in the present than it did during Hewatt's study, the direction of tidal height shift is ambiguous. The limpet *Tectura scutum* (B) shows a shift toward higher tidal heights in its distribution.

TABLE 6. Changes in tidal position of species that showed a significant shift in cumulative height distribution, based on Kolmogornov-Smirnov test ($P < 0.05$).

Species	Range†	Direction of shift‡	Central tidal height§	Abundance‖
Alia carinata	C	lower		*
'Collisella' scabra	C	ambiguous		*
Balanus glandula	C	ambiguous		
Clavelina huntsmani	C	lower		
Hermissenda crassicornis	C	higher	+ 0.27	
Littorina keenae	C	higher		*
L. scutulata	C	higher		*
Lottia digitalis	C	ambiguous		
L. limatula	C	higher		
L. pelta	C	ambiguous		*
Mytilus californianus	C	higher	+ 0.22	*
Pachygrapsus crassipes	C	higher	+ 0.50	
Phascolosoma agassizii	C	lower		*
Pugettia producta	C	ambiguous		
Tegula funebralis	C	ambiguous		*
Anthopleura elegantissima clonal	N	higher		*
Crepidula adunca	N	ambiguous		*
Leptasterias hexactis	N	ambiguous		*
Tectura scutum	N	higher	+ 0.57	*
Amphissa versicolor	S	lower		
Tetraclita rubescens	S	higher		*

† C, Cosmopolitan; N, Northern; S, Southern.

‡ Direction of shift is inferred from charts of cumulative distributions. Those that appeared to shift higher in part of the intertidal and lower in another are labeled "Ambiguous." See Fig. 5.

§ Tidal heights are given in meters relative to MLLW for species that showed a significant change in central tidal height (t test, $P < 0.05$).

‖ Asterisks indicate species that showed a significant change in abundance ($P < 0.05$).

TABLE 7. Percent cover of *Pelvetia compressa* by plot.

Plot	Height† (m)	1996 cover (%)	"Band" in 1933‡
14	1.65	0	
15	1.43	5	
16	1.14	30	x
17	0.87	0	x
18	1.06	5	x
19	1.17	0	x
20	0.97	8	x
21	1.00	3	x
22	1.02	10	x
23	1.05	10	x
24	0.86	0	x
25	0.93	0	x
26	0.82	0	x
27	0.88	10	x
28	0.74	0	x
29	0.74	0	x
30	0.61	0	x
31	0.57	0	

† Height relative to Mean Lower Low Water.

‡ The "x" symbols denote presence of *Pelvetia*, reported by Hewatt (1937:181, Fig. 11) to be nearly 100% cover.

faunal changes extends across taxonomic boundaries, negating the notion that broad, range-related changes were due to suites of closely related species exhibiting similar changes in abundance. For all species, the likelihood of change was not related to life history trait (brooder, long-dispersal, or short-dispersal), as would be expected if changes in physical transport processes (such as changes in the magnitude and frequency of ENSO events) occurred in the 60 years between studies.

Community shifts are due to changes in intertidal habitat characteristics.—It is apparent from Hewatt's photographs and detailed drawings that the granitic substratum along the transect has not eroded significantly in the last 60 years. Rock shapes and features, such as channels and fissures detailed in Hewatt's drawings, are readily identifiable today. The abundance of small, movable boulders that provide refugia for many intertidal invertebrates may have changed. Hewatt reported that crevices in the granite substratum were filled with loose rocks. We found very few loose rocks or small boulders along the transect. These rocks may have been dislodged by the strong storms known to move intertidal and shallow subtidal boulders as large as 6 m^3 (Gunnill 1985, Dayton et al. 1989). Regardless of the mechanism, removal of this rubble may have contributed to the decline in 8 of 10 species known to inhabit under-rock habitat (Table 8). Notably, removing these species from the overall analysis does not significantly alter the pattern of range-related changes.

Vertical shifts in intertidal distributions confound interpretation of geographic range shifts.—Although our analysis documented little or no change in species' tidal height distribution, the resolution of our tidal height estimates is coarse. Even though the vertical relief of plots along the transect averaged 0.44 m, we assigned a single average tidal height to each plot to facilitate calculation of species' tidal ranges. Thus, small shifts in vertical distribution (i.e., within the range of a plot's vertical relief) were not detectable from these data.

Recent measurements of the *Balanus–Endocladia* zone at HMS first investigated by Glynn (1965) indicate that the lower and upper boundaries of the alga *Endocladia muricata* shifted an average of 0.40 m and 0.18 m lower, respectively, at HMS (S. Gilman, R. Sagarin, A. Simons, J. Barry, and C. Baxter, *unpublished data*). Many small species that take refuge in *Endocladia* and other turf algae are likely to be most affected by this shift. Because Hewatt did not quantify algal abundance or its associated macro-fauna, we cannot quantify changes in these groups.

Anthropogenic environmental changes have resulted in invertebrate community shifts.—Direct anthropogenic effects on the transect are expected to have been minor during the period between Hewatt's investigation and ours. Public access to Hopkins Marine Station has been restricted since it relocated to its current site at Cabrillo Point in 1917. Taking of marine plants and invertebrates in the intertidal and shallow subtidal (to 17.7 m, or 60 feet) habitats at Cabrillo Point has been prohibited (except under special permit for scientific study) since the site was designated as a Marine Life Refuge by the California State Legislature in 1931, approximately the same time Hewatt began his study. Impacts from the sardine fishery effluent and sewage outfalls are also expected to have been minimal. Effluent from canneries was localized so that the intertidal area at HMS was not directly impacted even by the nearby Hovden cannery, the present-day site of the Monterey Bay Aquarium (Eugene Haderlie, *personal communication*).

Human protection of the harbor seal *Phoca vitulina richardii* may have had an impact on intertidal plants and animals through seal haul-out behaviors, nutrient enrichment (by urine and feces), and temperature changes due to shading, although the magnitudes of these effects are unknown (Boal 1980; G. Horng and S. Hayhurst, *unpublished data*). Although the number of seals hauled out at HMS has increased since they first appeared in the early 1970s, most seals haul out near Seal Rocks or West Beach, far from the transect (see Fig. 1A), and their effects on the invertebrate assemblage are likely to be minimal.

Patterns of community changes have arisen from indirect species interactions.—Changes in species' abundances may arise from direct responses to physical factors (e.g., sea temperature) or biological interactions (e.g., changes in predator or prey densities, or changes in biological habitat such as algal cover or host species densities) (Connell 1961, Paine 1966, 1992, Menge and Sutherland 1976, Connell 1983). Direct responses may induce a cascade of indirect impacts within an interaction web. In an extensive review of studies of community changes, Menge (1995) found that 40–50% of

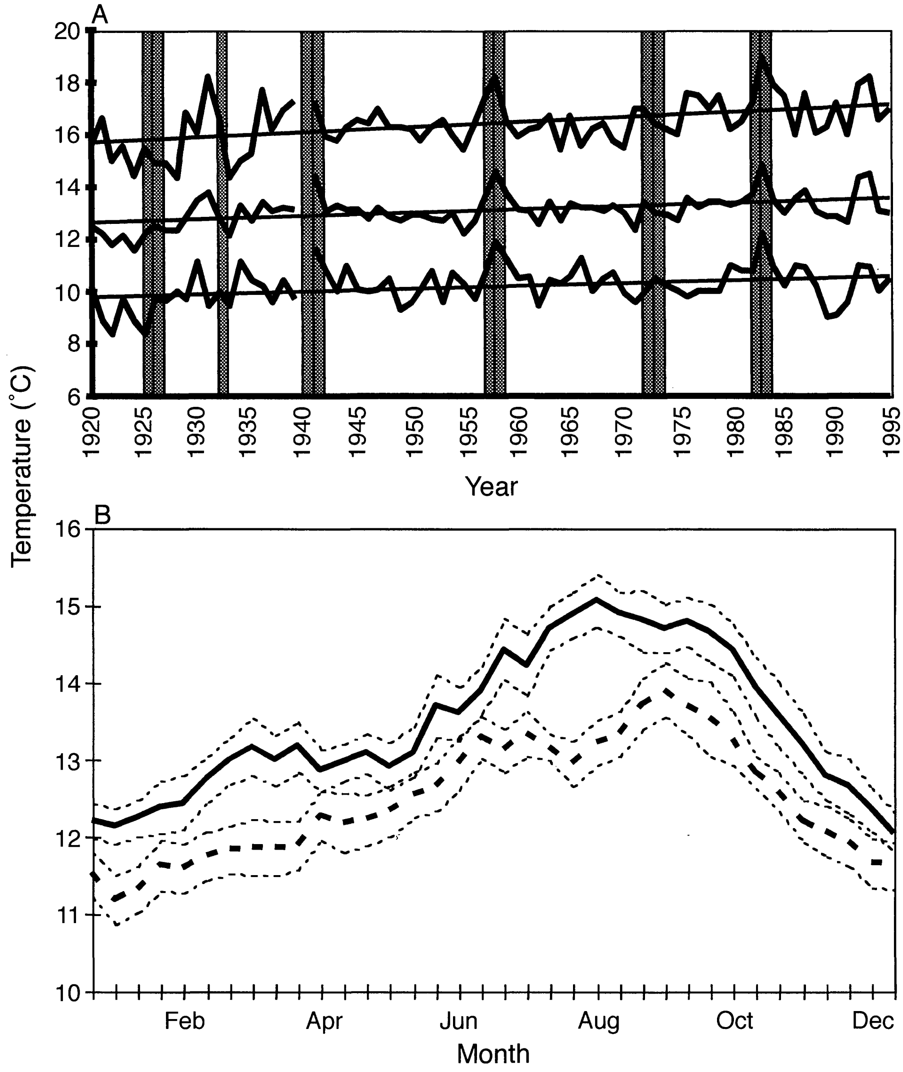

FIG. 6. (A) Plot of annual maximum, mean, and minimum shoreline ocean temperature recorded at HMS from 1920 to 1995. Gray vertical bars indicate strong ENSO years. Slopes for maximum, mean, and minimum temperature regressions are 0.0199, 0.0125, and 0.0104, respectively. (B) Monthly averaged shoreline ocean temperatures for HMS for the 13 yr preceding this study (solid line) and the 13 yr preceding Hewatt's study (heavy dashed line). Small dashed lines are ±1 SE.

changes seen in communities after a perturbation could be attributed to indirect effects. Furthermore, indirect effects are more likely to be responsible for population changes in long-term studies, such as this one, than in short-term studies (Wootton 1992). Dramatic changes in predators, host species, and algal cover have occurred at HMS since Hewatt's study, and it is likely that these changes have altered both direct and indirect interactions among species.

Two important top predators have returned to Hopkins Refuge area since the time of Hewatt's investigation. The sea otter, *Enhydra lutris,* which repopulated the HMS area in 1963, is a voracious predator of invertebrates. According to records kept by the Monterey Bay Aquarium since 1985, one male and three female otters routinely feed in the Hopkins Marine Life Refuge. The great majority of their prey at HMS is mussels (*Mytilus* sp.; Michelle Staedler, *unpublished data*). They have occasionally been observed to feed on purple urchins (*Strongylocentrotus purpuratus*), sea stars (*Pisaster ochraceus*), crabs (*Pugettia* sp., *Cancer* sp.), abalone (*Haliotis* sp.), and kelp snails (*Astraea* sp.) near HMS. Although urchins, sea stars, crabs, and mussels all decreased significantly in the outer plots of the transect (Table 9), otters forage only rarely in these plots (R. Sagarin, *unpublished observation*). The outermost plots that we surveyed do not extend into the extensive mussel beds and surrounding kelp forest, where the impact of otters is likely to have been greatest (VanBlaricom 1988). Because the prey species have relatively open populations due to their planktonic larval phase; otter predation in the areas outside the transect would not necessarily lead to declines in prey recruitment on the transect. It is thus difficult to assess

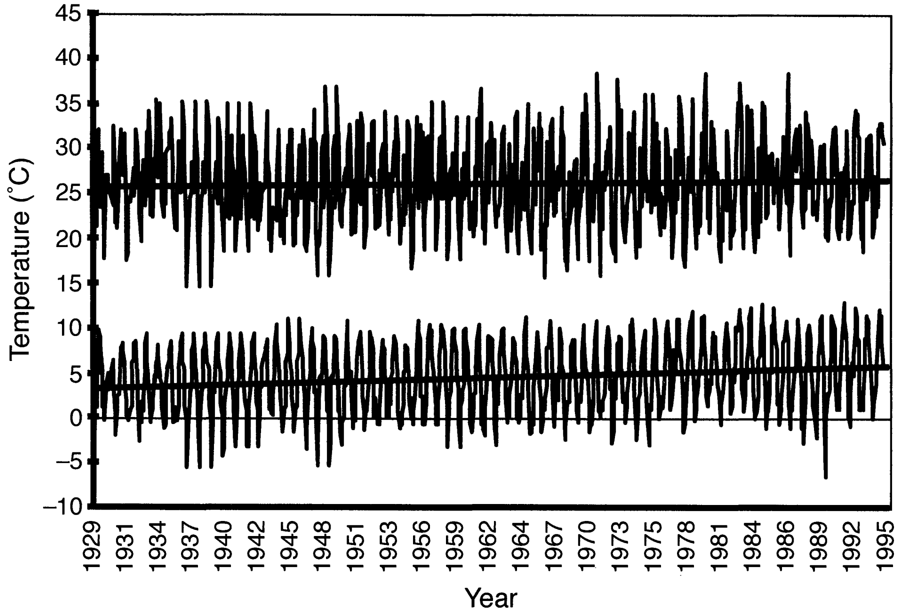

FIG. 7. Air temperature for Monterey Bay from National Climatic Data Center data. The plot of predicted Monterey air temperature from 1929 to 1995 is based on regressions from three nearby stations. Slopes of maximum- and minimum-temperature linear least-squares regressions are 0.0017 (R^2 = 0.0023) and 0.0057 (R^2 = 0.0355), respectively.

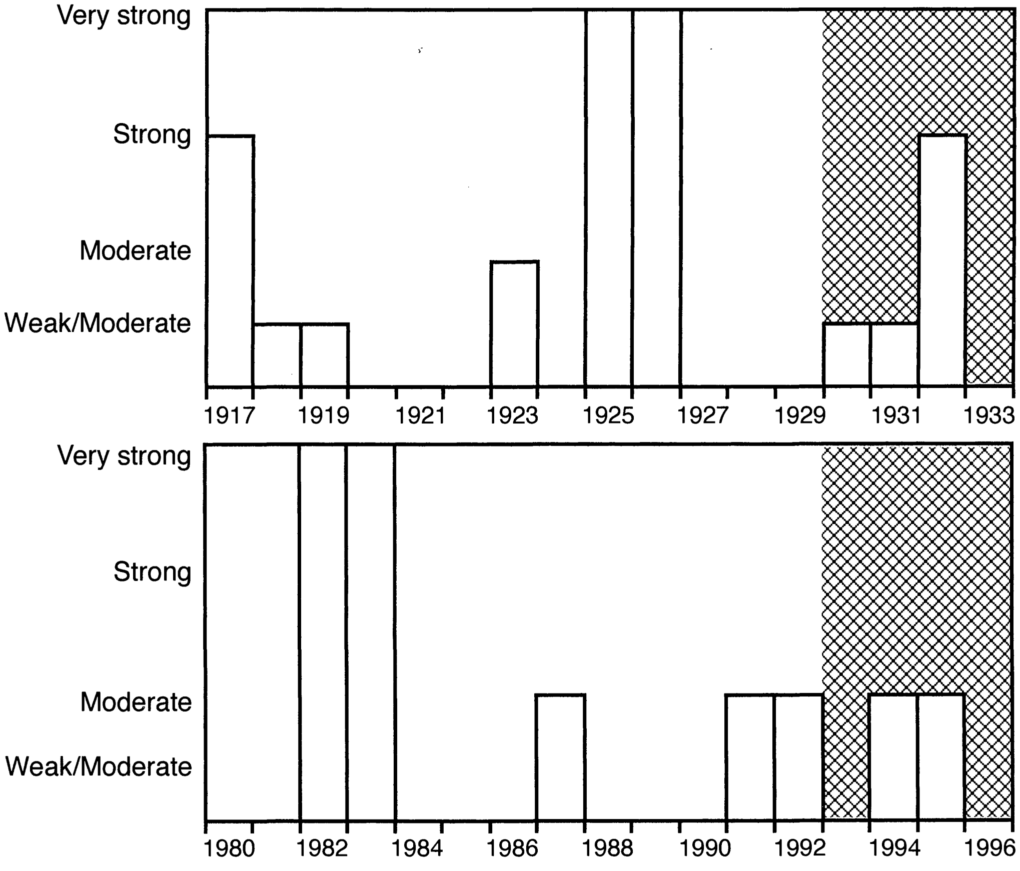

FIG. 8. Strength of ENSO events prior to Hewatt's study (top) and prior to this study (bottom), based on Quinn (1987) and Vernon Kousky (*personal communication*). Hatched areas represent survey periods for each study.

TABLE 8. Changes in species that use under-rock habitat.

Species	Range†	Change‡	Signif-icance	*P*
Alpheus clamator	S	–	*	0.05
Amphipolis pugetana	C	–	*	0.005
Cancer antennarius	C	–		0.08
Cancer productus	C	–	*	0.03
Hemigrapsus nudus	C	–		0.1
Hipponix cranioides	C	–	*	0.05
Leptasterias hexactis	N	–	*	0.006
Pachycheles rudis	C	–	*	0.001
Petrolisthes cinctipes	N	–	*	0.002
Phascolosoma agassizii	C	–	*	0.002

† C, cosmopolitan; N, northern; S, southern.

‡ Minus signs indicate a decrease in abundance between Hewatt's study and the present study.

* $P < 0.05$.

TABLE 9. Change in otter prey species in the low quadrats.

Species	Range†	Change‡	Signif-icance	*P*
Cancer antennarius	C	–		0.07
C. productus	C	–	*	0.02
Chama pellucida	C	–		0.1
Mytilus californianus	C	–	*	0.05
Pisaster ochraceus	C	–	*	0.02
Pugettia producta	C	–		0.22
Strongylocentrotus purpuratus	C	–	*	0.02
Tegula brunnea	C	+	*	0
T. funebralis	C	+		0.97
T. pulligo	C	+		0.24

† C, cosmopolitan.

‡ Plus and minus signs indicate an increase or decrease, respectively, in abundance between Hewatt's study and the present study.

* $P < 0.05$.

the effect of otters on populations on the transect. If otters did have an impact on these species, the overall pattern of range-related changes would not have been greatly affected, as all of the prey species are cosmopolitan in range.

The Black Oystercatcher, *Haematopus bachmani,* a shorebird that preys heavily on intertidal limpets (Hahn 1985), potentially influenced invertebrate abundances on Hewatt's transect. Although oystercatchers were observed occasionally at HMS in the 1960s (see Glynn 1965), a resident population of a single nesting pair has frequented HMS since 1979 (Alan Baldridge, *personal communication*). It is difficult to determine the effect of oystercatchers, if any, on species' abundances in this study. Although two limpet species preyed upon by oystercatchers decreased in abundance over the last 60 years, two others increased (Table 10). Foraging by oystercatchers may also confer an indirect benefit to nonprey species (see Wootton 1992). The increase in abundance of '*Collisella*' *scabra,* a limpet that is difficult for oystercatchers to dislodge (Hahn 1985, Hahn and Denny 1989), may result from reduced competition with other limpets that are preyed upon more heavily by oystercatchers.

Changes in abundance may also be mediated by interactions between symbiotic species. *Crepidula adunca,* one of two northern species that increased in abundance along the transect, is an epibiont on turban snails (*Tegula* sp.). Although the average abundance of *C. adunca* increased, its relative abundance on its principle hosts, *Tegula brunnea* and *T. funebralis,* did not change. Thus, the importance of *Tegula* sp. as a habitat resource confounds interpretation of changes in density for *C. adunca.*

Cover of foliose fucoid algae, especially *Pelvetia compressa,* apparently has decreased at HMS since the 1930s. Changes in algal cover are expected to have significant, direct effects on species that use algae for food or protection from desiccation and predation. Hewatt reported that rocks between 0.61- and 1.07-m tidal levels were covered with a "heavy layer of *Pelvetia* and *Fucus.*" He noted further that "[*Pelvetia*] is by far the most abundant alga in this region." (Hewatt 1934: 56). When Stephenson and Stephenson (1972) investigated the area at HMS in September and October 1947, they noted a "general dearth" of fucoid algae, including *Pelvetia, Fucus,* and *Pelvetiopsis.* We observe that this decline in fucoid algae has continued: *Pelvetia* is presently uncommon and patchy along the transect (Table 7) and at HMS in general.

The cause of the decline in *Pelvetia* is unclear. Although it has a published range from British Columbia to Baja California (Abbott and Hollenberg 1976), *Pelvetia* is not common north of San Francisco (Kozloff 1993; Carol Thornber, *personal communication*). Thus, *Pelvetia* would appear to oppose the observed trend of southern species increasing and northern species declining. Nevertheless, the overall change in the algal community at HMS has not been toward a more northerly assemblage. The Stephensons noted that the dearth of fucoids such as *Pelvetia* and dominance of red algal turfs at HMS (which still characterize the community today) make the site more closely resemble warm-temperate intertidal zones than the more northerly Pacific coast sites (Stephenson and Stephenson 1972).

The abundances of invertebrates associated with *Pelvetia* did not all decrease along the transect. Increased abundance of *Lepidochitona hartwegii,* a southern chi-

TABLE 10. Changes in oystercatcher prey species.

Species	Range†	Change‡	Signif-icance	*P*
Acmaea mitra	C	–	*	0.02
'*Collisella*' *scabra*	C	+	*	0.05
Lottia digitalis	C	–		0.13
Lottia limatula	C	–		0.27
Lottia pelta	C	+	*	0.02
Tectura scutum	N	–	*	0.05

† C, cosmopolitan; N, northern.

‡ Plus and minus signs indicate an increase or decrease in abundance between Hewatt's study and the present study.

* $P < 0.05$.

ton that uses *Pelvetia* almost exclusively for food and shelter (Andrus and Legard 1975, DeBevoise 1975), suggests that factors other than *Pelvetia* abundance influenced its local population.

Data obtained in retrospective surveys such as this are unsuitable for dissecting the effects and strengths of interactions among species. Likewise, the utility of techniques such as path analysis to identify indirect impacts is severely limited with these data (see Wootton 1994, Smith et al. 1997). Limited to data on abundance changes, we found that effects of strongly interacting species often appeared either ambiguous (e.g., some oystercatcher prey items increased and some decreased), or the opposite of that expected (e.g., *Lepidochitona* increased, whereas *Pelvetia* declined). Even when changes were well correlated with expectations of species interactions (e.g., *Crepidula* to *Tegula* ratios remained constant; otter prey declined), we could not be certain that species interactions were the causal mechanism for the observed changes. In no case did we find evidence of species interactions that could account for the entirety of the range-related pattern of change that we observed.

ENSO-related events caused the observed community shifts.—It is doubtful that ENSO events were responsible for the striking changes in the invertebrate community observed at HMS. Anomalous northward transport (Chelton et al. 1982, Johnson and O'Brien 1990), positive sea surface temperature anomalies (McGowan 1985), and increased recruitment to the intertidal (Gaines and Roughgarden 1987, Roughgarden et al. 1988) have been documented along central California during ENSO events (see studies cited in Lynn et al. 1995), but these events were similar in number and magnitude in the years preceding Hewatt's and our studies.

Moreover, the predicted effects of ENSO events are insufficient to explain the patterns of faunal change documented at HMS. ENSO-related oceanic transport should result in the greatest increase among southern species having long-lived planktonic larvae. Although few species were available for analyses, faunal changes were unrelated to life history characteristics, and several nonplanktonic species increased in abundance.

Southern species are often observed far north of their ranges during ENSO-associated oceanographic anomalies (see especially Pearcy and Schoener 1987, Lenarz et al. 1995), but these range extensions tend to be short-lived (Dayton and Tegner 1990) or to result in nonreproducing populations (Lenarz et al. 1995). Many temporary northward faunal extensions were reported during ENSO periods preceding and during Hewatt's study. For example, the sheephead (*Semicossyphus pulcher*), a wrasse that normally inhabits waters south of Point Conception, California, appeared in Monterey after both the 1982–1983 and 1992 ENSO events (Lenarz et al. 1995), and was also reported in the area after the 1930–1931 event (Walford 1931). Moreover, most reported ENSO-related range extensions concern higher vertebrates, and any effects on intertidal invertebrates are less well understood. Of 13 ENSO-related northward range extensions into Oregon reported by Pearcy and Schoener (1987), only three were invertebrates, only one was benthic, and none were intertidal species.

The few studies that have attempted to assess effects of ENSOs on adult intertidal populations have found little effect at the community level. Dayton and Tegner (1990) found few ENSO-associated effects on intertidal biota as a result of the very strong 1982–1983 ENSO. Any major effects were related largely to the unusually severe storms of the 1982–1983 event. Similarly, Gunnill (1985) found that the primary effect of the 1982–1983 ENSO event on southern California intertidal macroalgae was storm damage. Murray and Horn (1989) and Paine (1986) failed to detect any significant effects of the strong 1982–1983 ENSO event on intertidal communities in central California and on Tatoosh Island, Washington, respectively, even though nearshore pelagic effects were reported in both regions (Cannon et al. 1985, Pearcy and Schoener 1987).

The effects of ENSO events on oceanographic processes along the California coast vary greatly. Their common association with increased northward transport and warmer temperatures suggests that they may be important catalysts of range migration. ENSO-related effects should enhance rates of range migration along the eastern Pacific margin during periods of climate warming, through increased transport of southern larvae and elevated nearshore temperatures, leading to conditions favorable for southern species and unfavorable for northern species. ENSO effects are expected to counter the directional trend of range migrations during cooling periods. Nevertheless, ecologists' understanding of the response of intertidal populations to ENSO events remains limited, making it impossible to fully evaluate the role of ENSO in the observed changes to the HMS intertidal.

Community shifts are related to changes in upwelling intensity.—HMS is located in a well-studied, wind-driven coastal upwelling zone. Bakun (1990) argued that coastal upwelling in central California should intensify during climate warming, due to greater alongshore wind stress. Changes in upwelling intensity cannot be evaluated from nearshore sea temperature records available at HMS (Schwing and Mendelssohn 1997, Schwing et al. *in press*). Nevertheless, recent analysis shows that upwelling increased along the coastline surrounding Monterey Bay during the period 1946–1990 (Schwing and Mendelssohn 1997).

Changes in the HMS intertidal community are not consistent with the effects of increased coastal upwelling, which is predicted to affect intertidal populations in several ways. Intertidal sites adjacent to upwelling zones have shown enhanced algal productivity and increased herbivore biomass relative to non-up-

TABLE 11. Reported climatic periods as compared to those observed in HMS nearshore ocean temperature records.

Climatic periods	Reported regimes		Observed Monterey average temperature			
	Climate	Author; source	Regression slope	Minimum	Maximum	Mean
1920–1939	warm	Jones (1991);	+	9.74	15.88	12.69
1940–1966	cool	global sea	−	10.43	16.37	13.13
1967–1986	warm	temperatures	+	10.40	16.82	13.31
1920–1945	warm	U.S. Globec (1994);	+	9.94	15.98	12.83
1946–1975	cool	Scripps Pier	+	10.30	16.34	13.05
1977–1995	warm	records	−	10.43	17.11	13.46
1920–1960	warm	Southward (1995);	+	10.10	16.18	12.94
1960–1980	cool	southern Britain,	+	10.24	16.46	13.12
1981–1995	warm	English Channel	−	10.47	17.13	13.49

welling sites, presumably due to nutrient enrichment during some upwelling periods (Bosman et al. 1987). The integrated effects of increased upwelling and warmer ocean temperatures on community productivity are unclear. Although the total abundance of herbivores did not change along the transect in this study, we cannot determine from the data whether overall biomass of herbivores has changed.

Upwelling may also affect physical and biological barriers to settlement of planktonic larvae. Fronts generated at the intersection of upwelling plumes and California Current waters may inhibit onshore transport of invertebrate larvae (Roughgarden et al. 1988, 1991). Shoreward transport processes associated with internal waves, including surface slicks (Shanks 1983) or internal bores (Pineda 1991), are also diminished or disrupted by upwelled waters, thereby reducing rates of larval delivery to coastal sites. Although species with long-lived planktonic larvae are expected to be affected most greatly by these upwelling-related changes in transport processes, there was no clear pattern of faunal change linked to the life history of species.

Other evidence suggests that upwelling may affect species interactions in the intertidal. Sanford (1999) found that predation by the sea star *Pisaster ochraceus* along Oregon shores was reduced greatly during upwelling periods. Abundances of *P. ochraceus* declined significantly along Hewatt's transect, but it is unclear whether this is related to changes in upwelling, sea temperatures, otter predation, or some other factor. Any consequences of this decline to the prey species of *P. ochraceus* are unclear from the data.

Although linkages between upwelling and intertidal communities have been established in some intertidal systems (Bosman et al. 1987), the effects of long-term changes in upwelling intensity on the HMS intertidal are still poorly understood. None of the proposed effects of changes in upwelling intensity can account for the range-related pattern of change in species' abundances.

Mechanisms of change

The long-term warming of shoreline ocean temperature at HMS is consistent with predicted warming trends in sea temperature due to increased atmospheric greenhouse gas concentration (Fields et al. 1993, Lubchenco et al. 1993). This temperature increase is, nonetheless, smaller than other reports of ocean warming during this period (Strong 1989, Roemmich and McGowan 1995*a*).

The trend in shore temperature at HMS differs from that in several reports documenting warm and cool regimes during this century. Sea temperatures along the UK (Southward et al. 1995) were warm during 1920–1960 and 1981–1995. Jones et al. (1991) found global warming periods in 1920–1939 and 1967–1986 in both marine air temperatures and nearshore ocean temperatures. Records from the Scripps Institute of Oceanography pier indicate warm periods from 1917 to 1945 and 1977 to the present, with an intervening cool period (U.S. Globec 1994). Division of shoreline ocean temperatures into these time periods revealed a monotonic increase at HMS in annual mean, minimum, and maximum temperature between periods (Table 11). Lack of concordance of even the Scripps Pier records with the HMS time series is not surprising, because temperature fluctuations from areas as close as Monterey Bay and southern California often differ (MacCall 1996). Furthermore, Schwing (1993) found that sea temperature series from central California showed more gradual transitions toward warmer temperatures during this century when compared to the sudden regime shifts recorded in southern California. These differences in climate-change signals underscore the importance of local climatic data in studies of concordance between biological and climatic variables.

Dramatic changes in seasonal extreme temperatures in the 13 years prior to each survey of Hewatt's transect may have played a large role in the observed community shifts. If warming temperatures are responsible for invertebrate population changes at HMS, the considerably warmer summers preceding our recent survey may be a key factor. That seasonal temperatures, rather than average yearly temperatures, play a critical role in constraining latitudinal ranges has long been recognized by biogeographers (see especially Orton 1920, Setchell 1920, Hutchins 1947). More recently, Breeman (1990) proposed scenarios wherein ranges of northern European algae may contract in response to increased summer temperatures. Lewis (1986) has shown that extreme summer temperatures may prevent successful settlement of mollusk and barnacle species near their southern limits in the northeast Atlantic, while allowing extended breeding periods for species near their northern limits. If similar processes were to limit species' ranges along the California coast, then increased summer temperatures would result in lower abundances of species near their southern limits (our northern species) and higher abundances of species near their northern limits (our southern species).

Despite the strong correlation between increasing sea temperatures and range-related abundance changes, in the present study, we cannot identify specific mechanisms that could drive such changes. This reflects both the limitations of these data and a limited mechanistic understanding, by ecologists in general, of processes regulating range limits of species (Brown et al. 1996).

Evidence is emerging on physiological mechanisms related to heat stress that may serve to limit the geographic ranges of species. Stillman and Somero (1996) recorded under-rock temperatures in Oregon that were near the upper tolerance levels of porcelain crabs. They suggested that small increases in nearshore ocean temperature, similar to those documented here, could lead to elevated habitat temperature that could "profoundly affect species' distribution patterns at the latitudinal and vertical limits of the species' range." *Petrolisthes cinctipes,* a northern porcelain crab, declined along Hewatt's transect, perhaps due to increased temperature or to the disappearance of small boulders used by the crabs for shelter. Differences in the concentrations and induction of heat shock proteins (hsp) in northern and southern intertidal mussels suggest that northern species are more sensitive to warm temperatures (Hofmann and Somero 1996). The southern edges of some mollusk and barnacle species' ranges in the northeast Atlantic are also influenced by warm-temperature constraints on larval settlement (Lewis 1986). Likewise, insufficient summer warmth may cause recruitment failure toward the northern geographic limit of these species, and winter cold may lead to juvenile mortality (Lewis et al. 1982, Kendall and Lewis 1987). These examples suggest that a focus on both the response of adults to physiological stress and the cause of subadult mortality will be useful in identifying mechanisms responsible for range-related changes in species' abundances.

Our retrospective analysis of faunal changes at HMS represents "historical science" (sensu Francis and Hare 1994), employing correlation and related historical and observational information to evaluate community processes. This study reveals patterns of faunal change consistent with predictions of climate-driven shifts, and provides a baseline for future analysis of continued community reorganization. This type of retrospective analysis should ideally be paired with mechanistic studies to determine directly the roles and interactions of physiological, ecological, and physical pathways for climate-driven changes of biological communities.

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