SANDY BOTTOM COMMUNITIES AT THE END OF A COLD (1971-1975) AND WARM REGIME (1997-98) IN THE CALIFORNIA CURRENT: IMPACTS OF HIGH AND LOW PLANKTON PRODUCTION

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Abstract. There were highly significant changes in the structure of benthic infaunal communities at the end of the last cold regime (1976) compared to the end of the last warm regime (1999) in the California Current. The warm regime is characterized by much lower plankton production, which we argue is the primary cause of the degraded infaunal community at the end of the warm regime. In 1997-98, we resampled a depth gradient along a subtidal, high-energy sandy beach (6-24m) in Monterey Bay that was sampled for five years at the end of the last cold regime (1971-75). There was a dramatic decline in the total number species, number of individuals, and biomass by the end of the warm period. There was no overlap in benthic assemblages at all water depths between the decades in either non-metric multidimensional scaling ordination or cluster analysis. In the 1970s, the community dominants in the shallow crustacean zone, centered in 9 m, were pericarid crustaceans, including predacious phoxocephalid amphipods, haustoriid amphipods, and ostracods, which all live in the sediment. The amphipods, in particular, are well adapted to burrowing in sand. The numerical dominants in the deeper polychaete zone (18-24m) were large, sedentary polychaete worms. The largest was a tube-dwelling predator (*Nothria*) accounting for most of the biomass. The other was a suspension and surface deposit feeding polychaete worm, *Magelona*. By the 1990s, the most abundant crustacean was a small, swimming amphipod; and the most abundant polychaetes were small, relatively mobile, and deposit feeding. This trend from large size, sedentary, and suspension feeding to smaller size, higher mobility, and deposit feeding also characterizes infaunal shifts from the food-rich continental shelf into the food-poor deep sea. The dominant polychaetes had more opportunistic life histories, and shallow faunal zones extended into deeper water in the 1990s. If global warming continues, the ongoing cold regime may be less productive and the sandy bottom communities should not develop the species composition and high diversity, abundance, and biomass observed in the 1970s.

Keywords: Pacific decadal oscillation, benthic infaunal community structure

INTRODUCTION

There were likely four interdecadal regimes in the Northeast Pacific in the last century shifting between cold and warm states in the California Current: 1900-1924, 1925-1946, 1947-1976, and 1977-1999 (Mantua et al. 1997, Francis et al. 1998, Peterson and Schwing 2003). Another shift was reported in 1989 (Mantua and Hare 2002), but it was not accompanied by a persistent change in plankton production observed since 1999 (Peterson and Schwing 2003). The regime shifts are linked to variations in the position and strength of the Aleutian low-pressure system resulting in large-scale changes in wind patterns and ocean temperature. The two major domains of the Northeast Pacific, the California Current and the Gulf of Alaska, fluctuate out of phase (Mantua et al. 1997, Francis et al. 1998, Hare et al. 1999): when one is productive the other is less productive. The Pacific Decadal Oscillation describes these interdecadal shifts in climate variation (Mantua and Hare 2002, Mantua et al. 1997), which Chavez et al. (2003) call El Viejo, an excellent contrast to the more frequent El Niño-Southern Oscillation (ENSO). El Viejo caused often abrupt changes in marine ecosystems that are best documented in fisheries and plankton, but also birds and mammals (e.g., Roemmich and McGowan 1995, Brodeur et al. 1996, Mantua et al. 1997, Veit et al. 1997, Francis et al. 1998, McGowan et al. 1998, Anderson and Piatt 1999, Beamish et al. 1999, Mackas and Tsuda 1999, Vandenbosch 2000, Chavez et al. 2003). Warm regimes in the California Current are characterized by sharper thermoclines, greater stratification, less mixing of deep, nutrient-rich waters into the photic zone, and lower planktonic production. There is also more import of relatively warm water from the north. Cold regimes have the opposite characteristics (Francis et al. 1998). After the shift to a warm regime in 1977, zooplankton biomass doubled in the Alaskan Current (Brodeur and Ware 1992) and decreased 70% in the then warm California Current (Roemmich and McGowan 1995).

There is less information on how marine bottom communities respond to the ecologically important regime shifts in the Northeast Pacific. We know El Niño events (Dayton and Tegner 1984, Tegner and Dayton 1987, 1991) and longer-term oceanographic trends (Tegner et al. 1996, 1997, Dayton et al. 1999) have profound impacts on kelp forests in Southern California. There are correlations between decadal climate change and variations in shallow-water sedimentary communities in the Atlantic Ocean (Kröncke et al. 1998, Tunberg and Nelson 1998); and in the deep sea off California and in the Atlantic (Smith et al. 2006).

We therefore expect significant variations in the structure of benthic infaunal communities living on the continental shelf at the end of a cold and warm regime in the California Current. These two periods are decadal extremes in primary and secondary production. Oliver et al. (1980) sampled along the subtidal, high-energy sandy beach in Monterey Bay from 1971-75, just before the end of the last cold period, which ended in 1976 (Mantua et al. 1997). They sampled along a depth gradient from behind the surf zone (6m) to 24m (Figure 1). In the first year, they sampled at monthly intervals to document seasonal variation, determined that the main seasonal patterns could be captured by sampling from the four major seasons, and therefore sampled quarterly throughout the remainder of the study. They sampled along two depth transects in the center of Monterey Bay, but the longest time
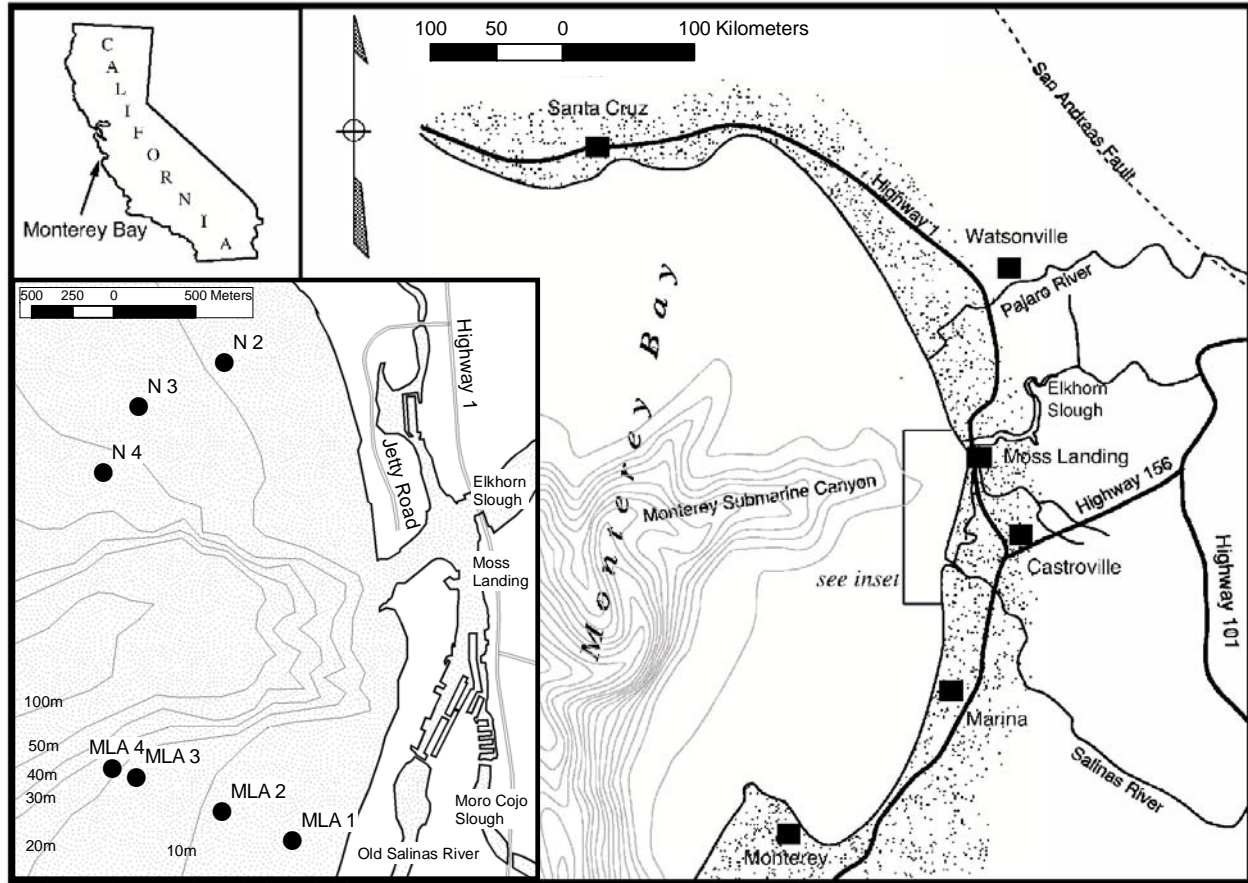
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FIGURE 1. Map of study site showing location of historical transects revisited in this study.

series was along the southern transect (MLA). Spatial (three to four water depths along two transects) and temporal (seasonal sampling over five years) fluctuations in benthic communities were thus measured when the ocean was colder and more productive.

This paper compares samples taken at the end of a warm period (1997-98) in the California Current, after 20 years of low ocean production, to data from the high production regime ending in 1976 (Oliver et al. 1980). The warm regime probably ended in 1999 (Peterson and Schwing 2003), and by 1997-98 all of the major measures of community structure fell outside the observations in the 1970s. After more than two decades of low availability of planktonic food, the sandy bottom communities were significantly degraded.

METHODS

Benthic infaunal communities were resampled at the same stations and seasons, using the same techniques, as Oliver et al. 1980 (Figure 1). We resampled two transects, one on the north and one on the south (MLA) side of Monterey Canyon (Figure 1). The complete depth gradient was resampled once along the north transect in September 1997 (9, 18, and 24m), and along the south transect in July 1997 (6, 9, 18, and 24 m). The summer and early fall were selected because the benthic communities had a relatively high biomass, abundance, and diversity throughout this period (Oliver et al. 1980). Since the 1970s sampling was most extensive along the south transect, seasonal samples were collected from this transect from the

center of the two major faunal zones. The 9 m and 18 m stations were sampled in July 1997, September 1997, December 1997, and May 1998. Six replicate diver-held cores (core area= 180 cm^2, 15 cm deep) were taken at each depth and time, and were washed over a 0.5 mm screen. Invertebrates were sorted from the screen residues, identified to the lowest possible taxon, and the number of individuals per taxon recorded with qualitative observations of individual size and sample biomass. Surface sediments (top 2 cm) were collected for measuring grain size distribution. We also made more than a dozen scuba dives along the depth transect between the two quantitative sampling periods collecting cores and other samples. These observations were made in the mid 1980's until the quantitative sampling in 1997-98. Finally, we taxonomically updated the historical quantitative data collected from 1971-75 to make these data directly comparable with the data collected in 1997-98.

Patterns in species composition and relative abundance for the two decades (1971-75 and 1997-98) were displayed using a cluster analysis and non-metric multidimensional scaling (MDS) ordination from PRIMER v.5 (Clarke and Gorley 2001). Some analyses utilized means or sums of replicate data. We achieved a stress value of 0.11 for the MDS. Stress indicates how faithfully the higher-dimensional relationships among the samples are represented in a two-dimensional ordination plot. This stress is low enough to provide detail in the MDS plot and to minimize misinterpretation from higher-dimensional solutions. There are no meaningful absolute units for the resulting axes. Points that are close together represent
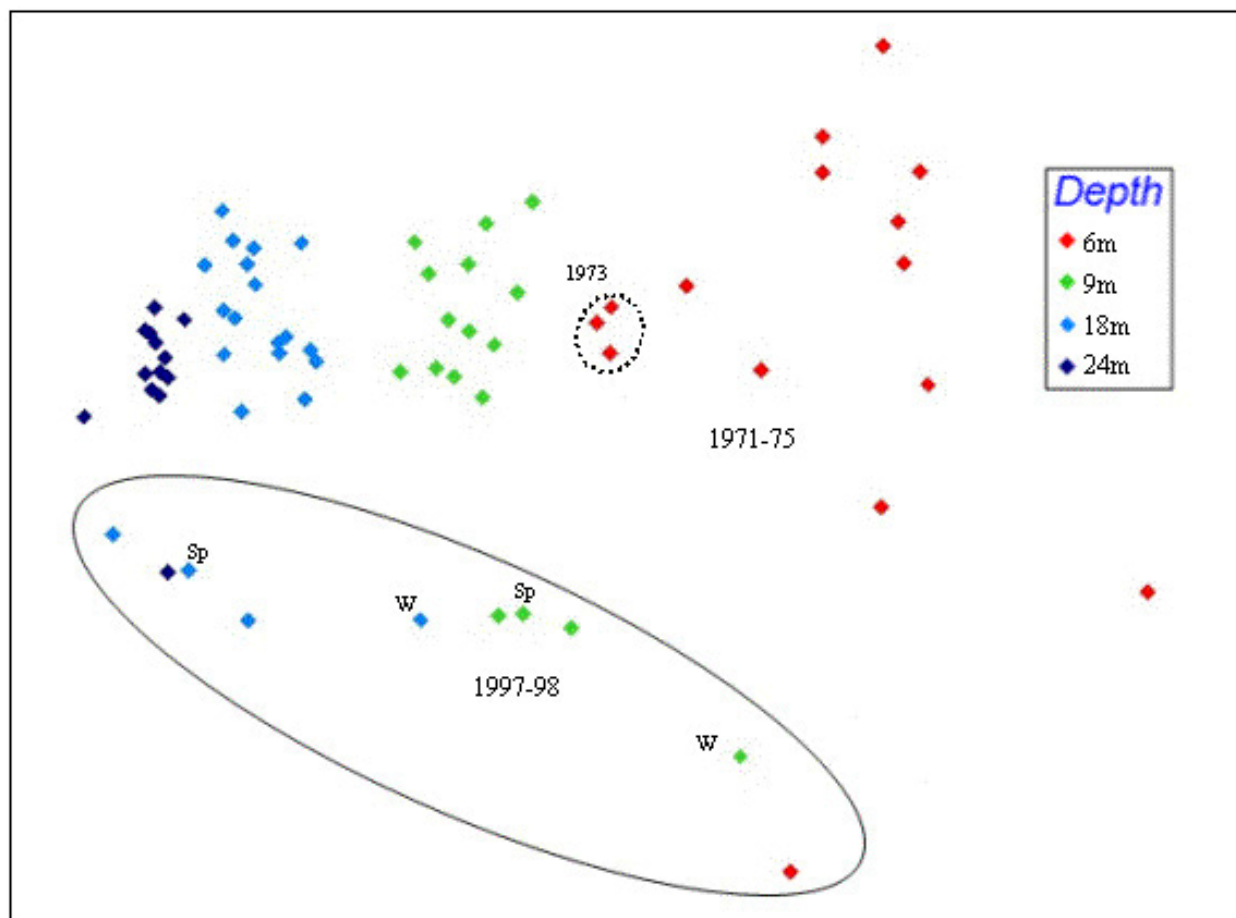
FIGURE 2. Separation of benthic infaunal communities in Monterey Bay by water depth and by decade using a non-metric Multi-Dimensional Scaling Analysis. W= Winter: Sp= Spring. Samples from 6m in 1973 are circled to show that they are between the other 6m and 9m samples. (Stress = 0.11)

samples that are most similar in species composition, while points that are far apart correspond to samples that are most different, based on Bray-Curtis similarity coefficients. To evaluate differences in species number and abundance between the two decades and compare selected species and species groups we conducted Analysis of Variance (ANOVA) using JMPIN Version 4.0.2 (SAS Institute 2000). In these analyses, we used a 2-way crossed layout where the main treatment of decade was imposed on the blocks of four water depths (n=502, df=494).

We used the Simpson's index (Simpson 1949) to document relative dominance patterns among species in each community (water depth). The index is scaled from 0 to 1: higher numbers indicate greater dominance.

We calculated a disturbance index (Hunt et al. 2001) used to estimate community response to environmental stress, usually from anthropogenic disturbances. The index depends mostly on number of species and the abundances of disturbance sensitive and tolerant species. Other quantitative indices, based on similar community metrics that are known to vary from disturbed to less disturbed habitats, are used to assess the health or biologic integrity of benthic communities (Weisberg et al. 1997, Karr and Chu 1999, Maurer et al. 1999, Hunt et al. 2001). These indices are developed and widely used for benthic invertebrates living in sedimentary habitats-almost always to assess the impacts of human pollution. One

of the most common human disturbances assessed is organic enrichment from sewage disposal. The index is composed of weighted sums of 3 metrics: community parameters (number of crustacean species, number of crustacean individuals, number of mollusc species, total number of species), three positive indicator species (*Rhepoxynius fatigans*, *Magelona sacculata*, *Tellia modesto*) known to decrease with disturbance, and three opportunistic negative indicator species (*Americhelidium shoemakeri*, *Armandia brevis*, *Apoprionospio pygmaea*) known to increase with disturbance.

The disturbance index was calculated as follows (see Hunt et al. 2001). The total range for total fauna and number of crustacean species for each station was determined. The total number of species, the number of mollusc species, number of crustacean species, and number of crustacean individuals at each station were then converted to the percentage of the total range for these parameters. These numbers represent one-third of the disturbance index for each station. For the positive and negative indicator indices, the final index was weighted towards presence and absence of key indicator species, with abundance of each species given additional incremental weight. The abundance of each indicator species was transformed using a double square-root transformation to compress the range of values, and was then converted to a percentage of the total range. The percentages of the negative indicator species was summed and subtracted
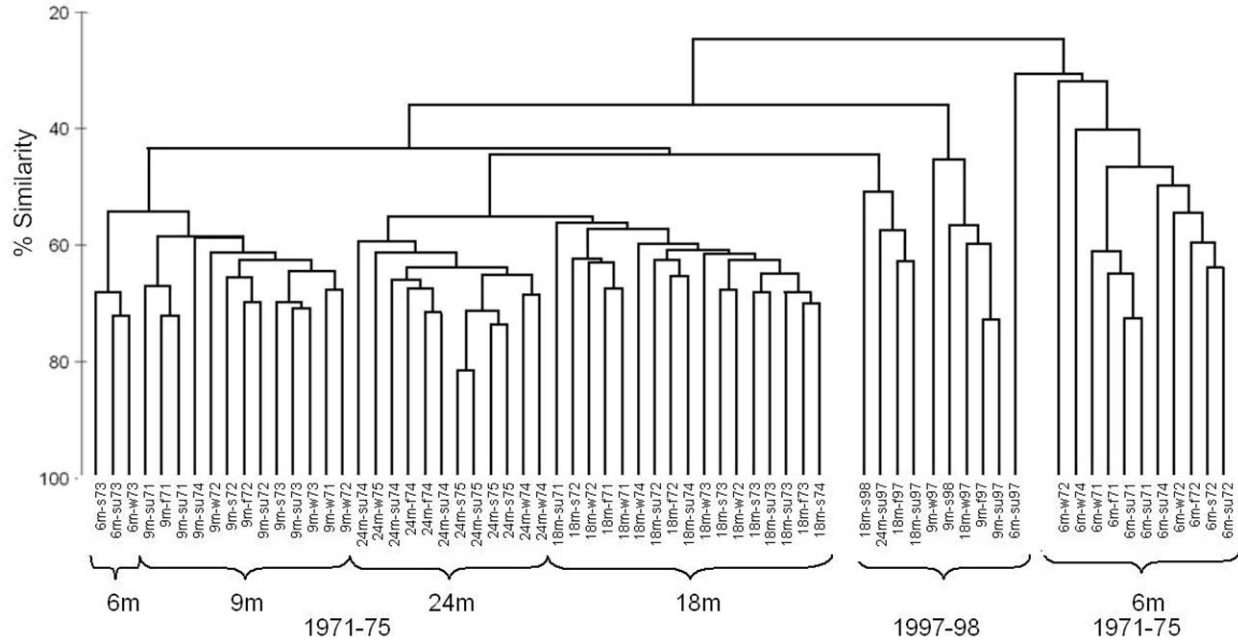
Figure 3. Separation of benthic infaunal communities in Monterey Bay by decade, year, season, and water depth using cluster analysis based on Bray-Curtis similarity (w=winter, s=spring, su=summer, f=fall).

from the percentages of the positive indicator species. This value was then converted into a percentage of the total for each station. The index is scaled from 1-0, less to greater stress or healthy to degraded in pollution settings (e.g., Weisberg et al. 1997, Karr and Chu 1999, Maurer et al. 1999).

We compared all data from the 1970s to all data collected in the 1997-98 survey for all the decadal comparisons except those in Table 3. The data in Table 3 are from only the summer months so we could compare these metrics at a time of peak community development (high abundance, diversity, and biomass) with less potential for confounding seasonal patterns (Oliver et al. 1980). Throughout the text, the genus name is used to refer to a single species within the genus.

RESULTS

South Transect Communities

The non-metric multidimensional scaling (MDS) diagram clearly separates samples by decade and water depth (Figure 2). There was no overlap in samples from the crustacean (6m and 9m) and polychaete zones (18m and 24m) in either decade, and no overlap between the decades. The only overlap in water depth was in the 1990s for the 18m and 24m stations (Figure 2). Otherwise, each water depth contained a distinct assemblage that did not overlap with other depths.

The MDS plot shows that for both 9m and 18m, where seasonal sampling was done, winter samples in the 1990s clustered closest to the adjacent, shallower station: the winter sample at 18m was closest to the 9m samples, and the winter sample at 9m was closest to the 6m samples (Figure 2). In addition, although there was an El Niño in 1997-98 that resulted in heavy rainfall mostly after the December 1997 sampling, the May 1998 samples (Sp in Figure 2) clustered closer to the July and September 1997 samples than any of

these samples clustered with the December 1997 samples (W in Figure 2).

The cluster analysis shows the same separation of assemblages by water depth and decade (Figure 3). In the 1970s, each water depth (6, 9, 18, 24m) contained separate clusters with no overlap. Each also clustered together, except for the 6m depth, which formed a distinct cluster from 1971, 72 and 74 (Figures 2 and 3). While there were shifts in relative abundance, the biggest difference in the 1973 samples was a much higher number of individuals, particularly among the three numerical dominants. The ostracod *Euphilomedes* was sixteen times more abundant; the gastropod *Olivella* was twenty times more abundant; and the amphipod *Eohaustorius* was twice as abundant in 1973 compared to the other years. With the exception of this 1973 cluster at 6m, samples did not cluster by year of sampling within each decade or by season (winter, spring, summer, fall). Unlike the 1970s, there was some overlap in water depths among the 1990s samples: the winter sample at 18m clustered with all the 9m samples and the single summer sample at 24m clustered with the other 18m samples (Figure 3).

Considering the entire species list, the species composition at each water depth was similar between the two decades. There was no occurrence, for example, of uniquely cold or warm water species between the two decades, even though the 1970s was a cold period, and the 1990s a warm period. On the other hand, there were major changes in the relative abundance patterns between the decades at each water depth, as indicated by the MDS plot and cluster analysis (Figures 2 and 3). Table 1 shows the ten most abundant species in the clusters from 6m, 9m, and 18/24m for each decade. The deeper depths (18/24m), which are in the polychaete zone, were combined for comparing the decades, because these depths clustered together in the 1990s (Figures 2 and 3).

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TABLE 1. Ten most abundant species in each major Cluster group shown in Figure 3 (mean per core, N = number of sampling units). (C-crustacean, P-polychaete, M-mollusc, E-Echinoderm)

1971-75			1997-98		
6 m		n=139	6 m		n=6
Euphilomedes longiseta	C	16.21	*Americhelidium shoemakeri*	C	30.67
Eohaustorius sencillus	C	6.62	*Dendraster excentricus*	E	5.00
Apoprionospio pygmaea	P	6.56	*Eohaustorius sawyeri*	C	4.50
Olivella pycna	M	6.54	*Mandibulophoxus gilesi*	C	2.83
Rhepoxynius lucubrans	C	6.23	*Scoloplos*	P	2.33
Eohaustorius sawyeri	C	5.39	*Pacificulodes spinipes*	C	1.00
Armandia brevis	P	3.65	*Syllis*	P	1.00
Americhelidium shoemakeri	C	2.69	*Armandia brevis*	P	0.67
Phylo felix	P	2.25	*Cyclaspis nubila*	C	0.67
Scoloplos armiger	P	2.02	*Lamprops sp.*	C	0.67
9 m		n=111	9 m		n=30
Eohaustorius sencillus	C	22.49	*Zeugophilomedes oblonga*	C	9.60
Zeugophilomedes oblonga	C	20.01	*Eohaustorius sencillus*	C	7.10
Dendraster excentricus	E	14.32	*Americhelidium shoemakeri*	C	4.97
Rhepoxynius fatigans	C	14.13	*Eohaustorius sawyeri*	C	4.08
Rhepoxynius abronius	C	14.09	*Armandia*	P	3.33
Tellina modesta	M	13.64	*Rhepoxynius abronius*	C	2.20
Euphilomedes longiseta	C	8.86	*Mediomastus californiensis*	P	2.13
Armandia brevis	P	8.10	*Apoprionospio pygmaea*	P	2.00
Rochefortia tumida	M	7.54	*Lamprops sp.*	C	2.00
Euphilomedes carcharodonta	C	7.38	*Nephtys parva*	P	2.00
18/24 m		n=258	18/24 m		n=30
Magelona sacculata	P	17.21	*Mediomastus californiensis*	P	19.20
Mediomastus californiensis	P	12.28	*Apoprionospio pygmaea*	P	9.20
Tellina modesta	M	10.63	*Armandia brevis*	P	8.27
Euphilomedes spp.	C	10.00	*Notomastus tenuis*	P	3.87
Photis macrotica	C	6.25	*Nephtys cornuta*	P	2.83
Rhepoxynius fatigans	C	5.52	*Lumbrineris luti*	P	2.60
Nothria elegans	P	5.34	*Amaeana occidentalis*	P	2.37
Apoprionospio pygmaea	P	4.80	*Magelona sacculata*	P	2.17
Lumbrineris luti	P	4.51	*Tellina modesta*	M	2.00
Dendraster excentricus	E	3.92	*Zeugophilomedes oblonga*	C	1.83

TABLE 2. Mean number of individuals per core and standard error of the major taxonomic groups along the depth gradient in Monterey Bay in the 1970s and 1990s

Group	6 m				9 m				18 m				24 m			
	1971-75		1997-98		1971-75		1997-98		1971-75		1997-98		1971-75		1997-98	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Crustaceans	37.4	2.7	42.8	3.4	90.5	4.7	33.7	4.1	18.9	1.2	11.3	1.8	9.2	0.8	4.5	1.0
Polychaetes	10.7	1.1	7.0	1.2	31.5	1.8	12.2	1.3	62.1	3.0	60.1	6.6	75.3	3.1	74.3	9.8
Molluscs	8.2	4.5	1.0	0.5	29.4	3.1	2.4	0.5	23.2	2.2	6.8	1.1	13.6	1.4	3.5	1.5
Echinoderms	0.6	0.1	5.0	1.1	14.5	2.7	3.6	0.6	4.9	0.8	0.7	0.2	0.5	0.1	0.7	0.4
Other	0.6	0.1	0.2	0.2	2.0	0.2	1.3	0.4	6.6	0.7	2.4	0.3	10.7	0.6	7.3	4.4
Total Individuals	57.5	5.6	56.0	4.9	167.9	8.4	53.2	4.8	115.7	4.6	81.3	7.0	109.3	4.2	90.3	15.8
N	108		6		103		30		131		23		95		6	

The total numbers of individuals and species per sample were higher for most depths in the 1970s (Figure 4). Differences in total number of individuals were significant both between the two decades and among the four water depths (ANOVA, $p<0.0001$). Differences in the number of species were significant between decades, and also among water depths (ANOVA, $p<0.0001$). Since the decadal contrast is our primary concern and the community changes with water depth are well described and significant (Oliver et al. 1980), the remaining analyses focus on the decadal patterns.

Most of the decrease in numbers of individuals from the 1970s to the 1990s was caused by a decrease in molluscs and crustaceans (Table 2, ANOVA $p<0.0001$ for each group), except for the higher number of crustaceans (mostly the small amphipod *Americhelidium*) at 6m in the 1990s (Table 1). The molluscs were several times less abundant in the 1990s,
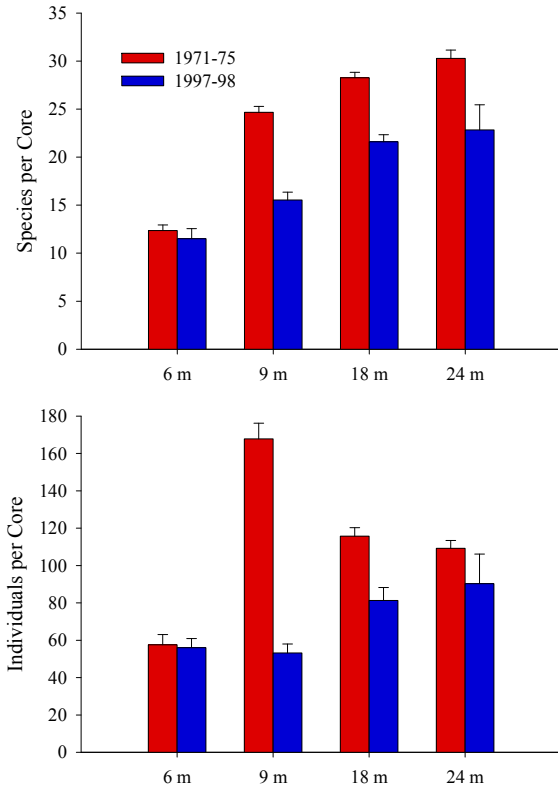
FIGURE 4. Mean and standard error for number of species (top) and individuals (bottom) per core along the depth transect in the 1970s and 1990s in Monterey Bay, based on sample sizes in Table 2.

TABLE 3. Changes in selected community metrics (number of species, number of individuals, Simpson's dominance index (λ), and disturbance index) with water depth and between the two decades, based only on samples collected during the summer months (N) when all depths were sampled in the 1990s.

Depth	Year	Species	Indiv	λ	Dist. Index	N
6 m	1970s	13.6	61.7	0.09	0.36	39
	1990s	12.0	61.3	0.30	0.11	6
9 m	1970s	25.9	178.3	0.08	1.00	39
	1990s	17.7	61.2	0.06	0.62	6
18 m	1970s	29.7	111.6	0.06	0.97	36
	1990s	22.7	100.0	0.08	0.65	6
24 m	1970s	35.8	130.9	0.05	0.79	28
	1990s	22.8	90.3	0.10	0.21	6

primarily the bivalve *Tellina*. The largest decrease in individuals was in the center of the crustacean zone at 9m (Figure 4), where the decrease in both molluscs and crustaceans was highest, as well as the decrease in very small, juvenile sand dollars (*Dendraster*), the only abundant echinoderm (Table 2). Changes in echinoderm abundance between the decades was also significant along the entire depth transect (ANOVA, p<0.0001). Polychaetes were less abundant at all depths in the 1990s, but all of the differences were more dramatic with the crustaceans and molluscs (Table 2). In contrast to number of individuals, most of the decrease in the number of species between the decades (Figure 4) was caused more by a decrease in the number of polychaete and molluscan species, not crustaceans.

While the decadal changes in the total numbers of individuals and species (Figure 4) were highly significant, ecologically and statistically, as were most of the changes in the major taxonomic groups (Table 2), the differences in the most abundant species were even more impressive and revealing (Table 1, Figures 5 and 6). Three major taxonomic groups dominated the crustacean zone in the 1970s: phoxocephalid amphipods (mostly species of *Rhepoxynius*), haustoriid amphipods (two species of *Eohaustorius*), and ostracods (species of *Euphilomedes* and *Zeugophilomedes*) (Oliver et al. 1980, Table 1). In the center of the crustacean zone at 9m, phoxocephalids were seven times more abundant in the 1970s; haustoriids were twice as abundant; and ostracods were three times more abundant (Figure 5). The decadal differences in these three dominant crustacean groups

were similar when all four water depths were considered (Figure 5, ANOVA p<0.0001).

One species of crustacean dramatically increased in abundance from the 1970s to the 1990s. The oedicerotid amphipod, *Americhelidum*, was over ten times more abundant at the 6m station in the 1990s (Figure 6, Table 1). The difference between the decades was highly significant for the entire depth transect (ANOVA p<0.0001).

Two species of molluscs were among the top ten most abundant species along the depth transect, *Olivella*, and the small bivalve, *Tellina* (Table 1). *Olivella* was primarily found at 6m, and sometimes in dense patches that were visually conspicuous to divers. Apparently, the 1973 cluster at 6m was from a similar high density that persisted throughout this year (Figures 2 and 3). None were captured in the six cores taken in July 1997, which certainly could be related to this small sample size. *Tellina* was the most common and abundant mollusc along the depth gradient in the 1970s (Table 1). This bivalve decreased dramatically at all water depths by the 1990s (Figure 6, ANOVA p<0.0001).

Magelona and *Nothria* were among the three most abundant polychaete worms in the polychaete zone in the 1970s (Table 1). Both were also among the largest species accounting for much of the biomass here (Oliver et al. 1980). An adult *Nothria* is about ten times the weight of an adult *Magelona*, which is several times larger than the three numerically dominant polychaetes in the 1990s. *Nothria* was thus the largest of the common and abundant animals collected from the depth transect. The abundances of both species decreased significantly along the entire depth transect between the two decades (Figure 5, ANOVA p<0.0001). In the polychaete zone, *Magelona* was more than ten times less abundant, and *Nothria* fives times less abundant by the 1990s (Table 1, Figure 5).

By the 1990s, the three most abundant species in the polychaete zone were *Armandia*, *Apoprionospio*, and *Mediomastus* (Figure 6). In general, these species increased in abundance between the decades, but not nearly as much as the community dominants from the 1970s (*Magelona*, *Nothria*, *Tellina*, and the three crustacean groups) decreased in number
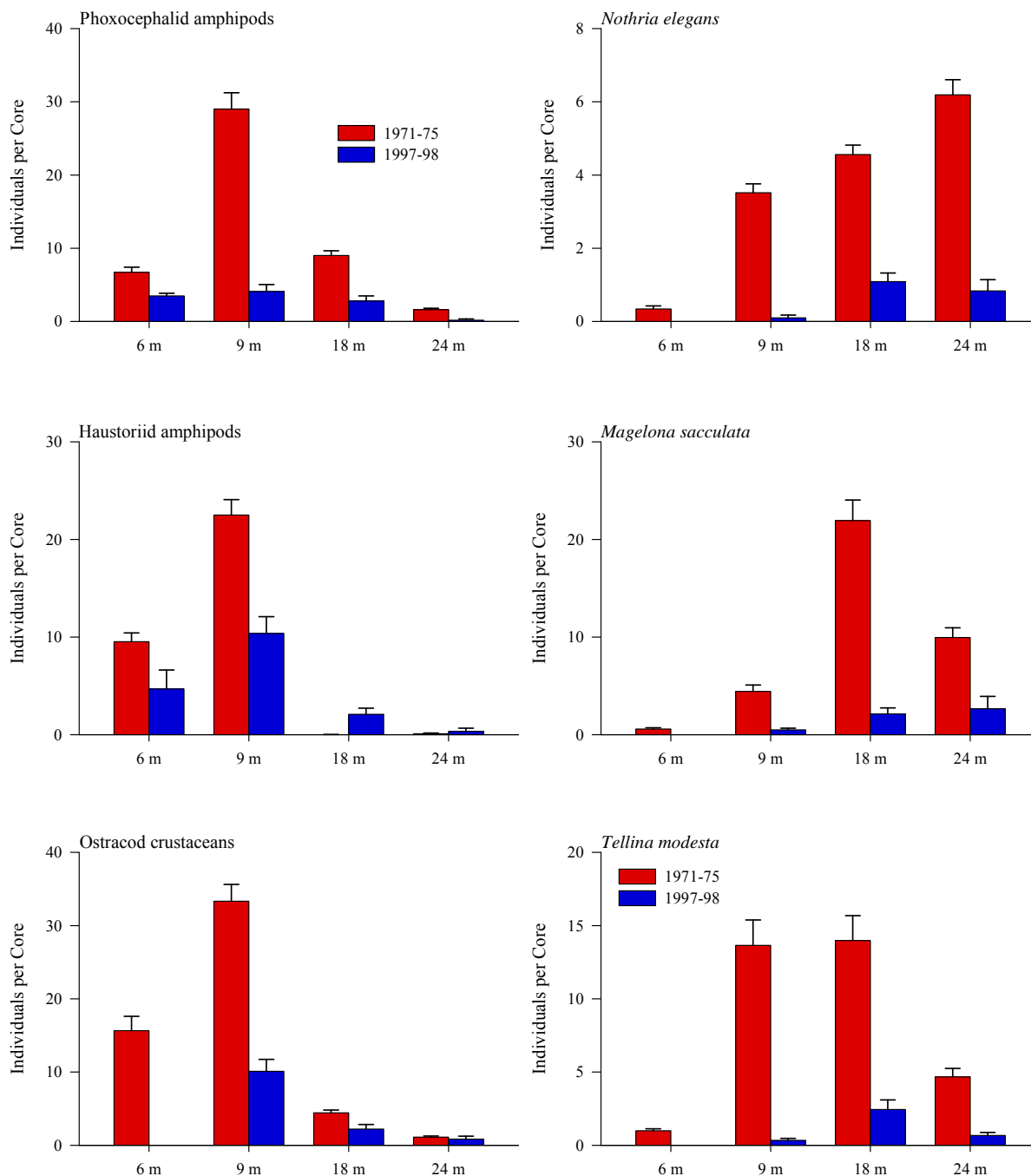
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FIGURE 5. Decreases in abundant taxa between the decades, including amphipod and ostracod crustaceans, two polychaete worms, and the bivalve, *Tellina*. Means and standard errors (sample numbers shown in Table 2).

by the 1990s (Figures 5 and 6). The new dominants shifted in rank compared to the dramatic decline in the abundances of dominants in the 1970s (Figures 5 and 6). Nevertheless, the decadal differences for the 1990s dominants were statistically significant: *Apoprionospio*, *Armandia* and *Mediomastus* (p<0.0001).

The primary pattern we observed during qualitative observations from the mid 1980's until the 1997-98 sampling

was the decrease in crustaceans in the crustacean zone (9m). During this period, several colleagues wanted us to collect phoxocephalid amphipods for use in developing a standard marine bioassay for the Environmental Protection Agency. Unlike previous work throughout the 1970s (Oliver et al. 1980, 1982, Oakden et al. 1984 a, b, Slattery 1985), when these crustaceans were abundant, we were unable to collect nearly as many from the mid 1980's. Earlier we supplied
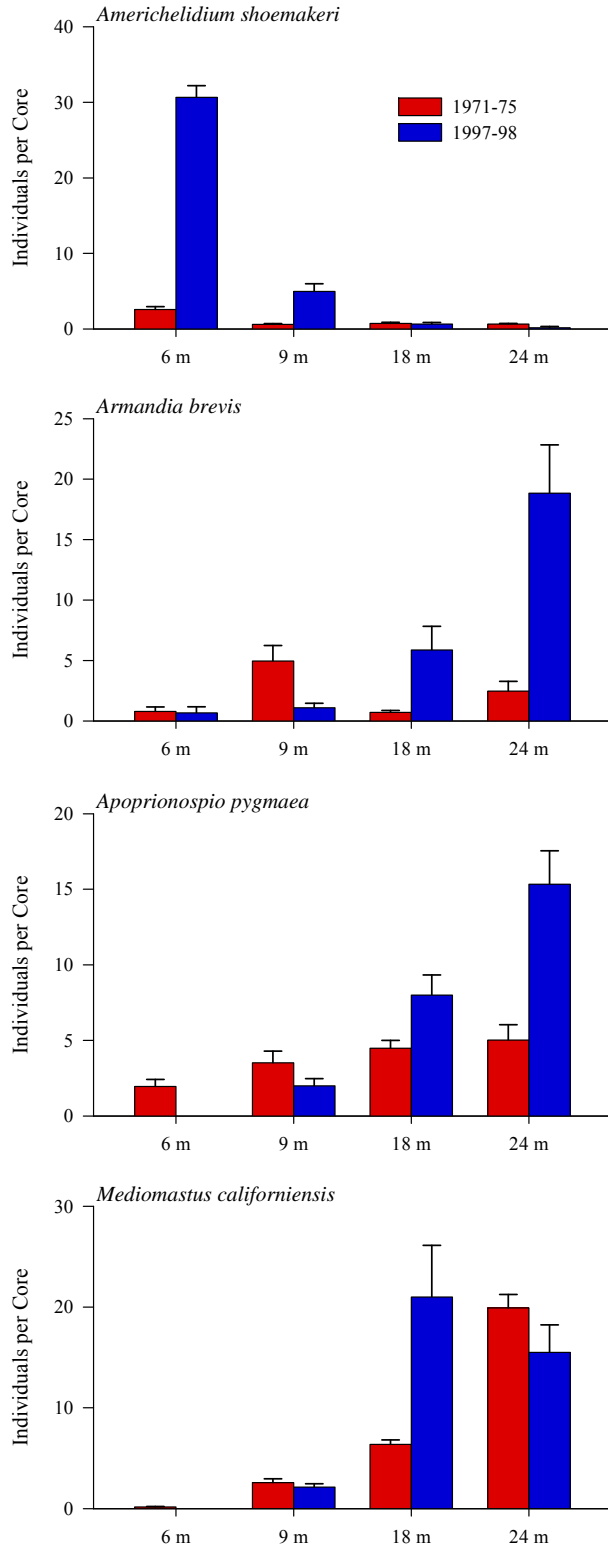
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FIGURE 6. Numerically dominant species at 6 m and 18/24 m in the 1990s compared to the 1970s. Means and standard errors (sample sizes shown in Table 2).

colleagues with large numbers of live animals. Later, we collected so few that our colleagues found alternate collecting

areas along the coast of Oregon. The haustoriid amphipods and ostracods were less abundant as well.

There were only slight changes in dominance between the decades, except at 6 m (Table 3), where the amphipod, *Americhelidium*, was five times more numerous than the second most abundant species by the 1990s (Table 1).

Disturbance indices can be based on excellent, robust natural history, including both species number and relative abundance as important metrics (Weisberg et al. 1997, Karr and Chu 1999, Maurer et al. 1999, Hunt et al. 2001). The disturbance index we used showed a remarkable decline between the decades at all water depths (Table 3). It was highest at 9m in the 1970s, because of the dominance of crustaceans here, particularly phoxocephalid amphipods. The number of crustacean species and the abundance of these amphipods are important index metrics (Hunt et al. 2001). This and similar indices are used to assess community health or biological integrity usually in relation to human-induced environmental stress. The index indicates dramatic degradation of community structure from the end of the cold period compared to the end of the warm regime (Table 3).

Finally, the data in Table 3 are from only the summer months so we could compare indices at a time of peak community development (high abundance, diversity, and biomass) with less potential for confounding and significant seasonal patterns (Oliver et al. 1980). Nevertheless, the patterns in the summer data (Table 3) and the entire data set (Figure 4) were essentially the same for both the number of species and individuals.

North Transect Communities

The primary decadal contrast was made along the south transect, because there was more extensive sampling here in the 1970s. The north transect was exposed to significantly greater wave disturbance, because of wave refraction of the generally northwest swell in Monterey Canyon (Oliver et al. 1980). As a result, the center of the crustacean zone was located in deeper water (18m compared to 9m along the south transect), and the 6m depth was not sampled because of hazardous boat operations. The same general decadal changes were observed along the north transect as those described above along the south transect: lower numbers of species, individuals, and biomass by the 1990s. For example, there were over twice as many individuals present at every water depth in the 1970s compared to the 1990s (Table 4).

Physical Setting

Sediment grain size (south transect only) was similar at all water depths between the decades, including the gradual decrease in median grain size with increasing water depth (Table 5). Median grain size is shown in phi units, which are smaller with coarser deposits and larger with finer deposits. The percentage of sand and silt/clay follow similar trends with depth and by stations for both decades. Table 5 does not include sediments collected in May 1998, because this sampling period occurred after the record rainfall coincident with the 1997-98 El Niño, and we therefore wanted to show it separately. In May, median grain size was the finest observed during the 1990s (9m=3.96 and 18m=4.76). The silt/clay fraction was highest as well (9m=15%; 18m=19%). The deposit still became finer with increasing depth. The fines

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TABLE 4. Changes in the mean number of individuals per core between the decades along the northern transect.

Depth	Year	Total Fauna	Crustaceans	Polychaetes	N
9 m	1970s	102	60	20	14
	1990s	33	24	8	6
18 m	1970s	185	131	46	24
	1990s	74	52	18	6
24 m	1970s	151	98	43	22
	1990s	60	39	17	6

were deposited after the winter storm waves and were unlikely to persist until the next winter storms, which control grain size distribution along the wave-exposed beach (Clifton et al. 1971). There was no evidence for a response in the benthic community after the El Niño rains (Figure 2).

DISCUSSION

Pelagic Production and Benthic Community Structure

There was a dramatic difference between the benthic infaunal communities at the end of a cold regime in the California Current compared to the end of the next warm regime. The last cold period started in 1947 and ended in 1976 (Mantua et al. 1997). The last warm period started in 1977 and ended in 1999, when the system apparently shifted back to cold again (Peterson and Schwing 2003). Throughout millions of years, periods of cold in the ocean have been correlated with high plankton production, and periods of warm with relatively low production (Berger et al. 1989). In general, a colder ocean is better mixed, moving deep nutrients into the photic zone and increasing plankton production. A warmer ocean is more stratified, reducing nutrient inputs from below and creating less productive surface waters. This is the pattern of planktonic production in the California Current as it shifts between the warm and cold regimes every 20-30 years (Roemmich and McGowan 1995, Francis et al. 1998, McGowan et al. 1998, Chavez et al. 2003).

Highly significant ecosystem changes have been documented in relation to these regime shifts, primarily in pelagic ecosystems where the main impacts were on lower trophic levels working their way up the food web, bottom-up responses (Francis et al. 1998). There were also top-down responses like an increase in predatory fish at the expense of forage species that were important prey for marine birds and mammals, which subsequently decreased in numbers (Francis et al. 1998).

Like the pelagic ecosystem, the dramatic decline in planktonic production was likely to be the primary causal factor leading to the degradation of benthic infaunal communities at the end of the warm regime. Open-coast benthic communities in this shallow depth zone may be especially sensitive to changes in planktonic production. Our sampling was done from just behind the surf zone to 24 m along a high-energy, open-coast sandy beach. The depth of the most productive surface water in Monterey Bay usually extends to around 20m (Pennington and Chavez 2000). So, the bottom communities along the subtidal beach are bathed in the most productive planktonic communities near the surface of the ocean in a high-production upwelling center (Pennington and Chavez 2000, Chavez et al. 2003). This production has

the potential for coming into direct contact with the sea floor, where benthic animals can suspension feed on smaller food and capture larger zooplankton. During the cold regime, the bottom is exposed to greater production, phytoplankton and zooplankton, compared to the warm regime (Roemmich and McGowan 1995, Francis et a. 1998, McGowan et al. 1998, Chavez et al. 2003). The sandy bottom communities were thus shallow enough (<30m) to feed directly on dense planktonic communities from the photic zone in a highly productive upwelling center, Monterey Bay.

Life History and Disturbance

Our sampling was done just before the end of the last cold period (1971-75), and just before the end of the last warm period (1997-98). By the end of the warm, low production regime, benthic communities had significantly lower numbers of species and individuals (Figure 4), and lower biomass. Relative abundance patterns changed radically, and completely different assemblages were present at almost every water depth along the subtidal beach (Figures 2-6, Tables 1-4). During the cold regime, the numerically dominant populations in the crustacean zone were haustoriid and phoxocephalid amphipods that are well adapted to burrowing in sandy sediments (Slattery 1985) and ostracods that live in superficial sediments and are weak swimmers (Oliver et al. 1980). So, the dominant crustaceans were strongly associated with sediment. The phoxocephalids, which decreased by a factor of seven, are voracious top predators as well as deposit-feeding infauna (Oliver et al. 1982, Oliver and Slattery 1985). In contrast, the most abundant crustacean in the 1990s and the only crustacean to increase significantly over time was *Americhelidium*, a small amphipod that regularly swims into the overlying water (Oliver et al. 1980). It is not adapted to burrowing. It is an active swimmer, and also a scavenger and predator, but on much smaller prey. In Korea, a closely related species of *Synchelidium* mainly eats harpacticoid copepods, while the juveniles also eat copepod nauplii and nematodes (Yu et al. 2003). The local phoxocephalids, in contrast, often eat polychaete worms (Oliver et al. 1982). An adult *Americhelidium* is about ¼ the biomass of the most common phoxocephalid amphipod (*Rhepoxynius*).

The two numerically dominant polychaete worms that decreased dramatically between the decades in the deeper polychaete zone were relatively large and sedentary. The most abundant animal in the 1970s, *Magelona*, lives in a semi-permanent burrow and suspension feeds. The onuphid worm, *Nothria*, was the third most abundant polychaete and the biomass dominant in the polychaete zone. It lives in a sand tube and is active at the sediment surface as a scavenger, predator with large chitinous jaws, and a deposit feeder. One large *Nothria* has a greater biomass than all of the abundant amphipod and ostracod crustaceans combined from a normal sample. In contrast to the 1970s dominants, the three most abundant polychaetes in the 1990s were small species, and at least two of them more mobile. *Armandia* was the smallest, a highly mobile, surface-active species without a permanent tube or burrow. *Apoprionospio* is also surface active, a suspension and surface deposit feeder, living in a transient burrow or tube. *Mediomastus* is a subsurface deposit feeder, actively burrowing through the top 10 cm of the sediment.

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TABLE 5. Changes in sediment grain size along the depth gradient between the decades along the South Transect (1970s from Oliver et al. 1980).

Depth	Year	Median Grain Size	95% CL or range	Sorting Coefficient	% Sand	% Silt & Clay
6m	1970s	2.93	0.30	0.44	99	1
	1990s	2.31	n=1	0.67	98	2
9m	1970s	3.27	0.04	0.47	92	8
	1990s	2.98	2.66-	0.71	97	3
18m	1970s	3.39	0.05	0.38	94	6
	1990s	3.44	3.30-	0.94	91	9
24m	1970s	3.53	0.05	0.43	89	11
	1990s	3.68	n=1	1.03	86	14

Thus, among the crustaceans there was a shift from burrowing forms tied strongly to the sediment to much smaller swimmers, and the loss of a dominant predator group, the phoxocephalid amphipods, at all water depths. Among the polychaete worms, there was a shift to smaller, less sedentary species, and the loss an abundant suspension feeder and a large predator that dominated the animal biomass. Everywhere along the depth gradient the suspension-feeding and surface deposit-feeding bivalve, *Tellina*, decreased in abundance by the end of the warm regime. This is the same general trend moving from food rich (eutrophic) to food poor (oligotrophic) benthic environments, for example, from the continental shelf into the deep sea: less sedentary species, more mobility, smaller size, and often less suspension feeding with less food (Jumars and Fauchald 1977, Dayton and Oliver 1977, Fauchald and Jumars 1979). The large decrease in the size of dominant predator populations may simply be related to less prey, both in the plankton and the benthos.

In addition to changes in size and mobility, there were other shifts in life history patterns among the polychaete worms between the decades. The dominant polychaetes in the 1990s had more opportunistic life histories including the ability to respond rapidly to disturbance (Grassle and Grassle 1974). *Armandia* and *Apoprionospio* were among the first to colonize experimental substrates at small and large experimental scales as well as naturally disturbed bottoms (Oliver et al. 1977, 1980, Hulberg and Oliver 1980, Okey 1997, 2003). Their larvae were among the most abundant captured above the sea floor in collecting jars (Oliver et al. 1977, Hannan 1981). In addition, they occurred in habitats subjected to higher levels of natural disturbance (Oliver et al. 1980). *Mediomastus* also has a relatively opportunistic life history, less so than the two former species, and was found in more disturbed regions along environmental stress gradients, and early in succession following disturbance (Grassle and Grassle 1974, Oliver et al. 1977, Lenihan and Oliver 1985, Conlan et al. 2004). A similar life history occurs in the only crustacean (*Americhelidium*) that dramatically increased between the two decades. This species and other oedicerotid amphipods are well adapted for swimming and were among early colonists in disturbed sedimentary habitats (Oliver et al. 1977, Dauben et al. 1990, Lenihan and Oliver 1995). In Monterey Bay, *Americhelidium* is abundant in the surf zone as well as the turbulent region just offshore (Table 1), where wave-generated bottom disturbance is high (Oliver et al. 1980).

The disturbance index reflected this shift in life history patterns as well as the decrease in species density. At all depths, communities in the 1970s showed high index values that declined dramatically by the 1990s (Table 3), which is correlated with a significant decrease in planktonic food during the warm regime of El Viejo. This is the opposite of organic enrichment. Too much food (organic enrichment conditions) and natural phases of low levels of food (El Viejo) can both stress ecological communities.

Environmental stress gradients are often coincident with gradients in diversity (species density), abundance, and biomass in sedimentary habitats. Regions of high organic enrichment and related pollution generally have lower values, which increase away from the highest enrichment sites, although sometimes abundance can be high at enriched areas (Pearson and Rosenberg 1978, Stull et al. 1986, Hunt et al. 2001, Conlan et al. 2004). Diversity, abundance, and biomass decrease from dissipative to reflective sandy beaches, another gradient in environmental stress (Defeo and McLachlan 2005). A similar general pattern was observed along the wave-disturbance gradient in both decades in Monterey Bay and in other wave-controlled environments: lower diversity, abundance, and biomass with increasing wave disturbance (Oliver et al. 1980, McLachlan et al. 1984). We documented the same decreases in the present study from a food-rich, cold regime to a food-poor, warm regime in the California Current (Figure 4). There are also two studies that relate climate change (Atlantic Oscillation) to long-term variations in benthic infaunal communities. One concluded that climate-induced variations in primary production caused significant changes in the benthos (Tunberg and Nelson 1998). In the other, variations in climate-induced wave disturbance and other environmental stresses were linked to long-term changes in benthic communities (Kröncke et al. 1998).

There was little change in dominance from the 1970s to the 1990s, despite the significant decline in the total number of individuals at all depths, except at 6m (Table 3). In addition, dominance did not vary directly with total density of the fauna along the depth gradient in either decade (Table 3).

There was a subtle shift in zonation along the transect. By the 1990s, the distribution of several shallow-water groups spread into deeper water. These were the same relatively opportunistic groups that dominated by then, particularly *Armandia* and *Apoprionospio*, but also *Americhelidium*, which moved into 9m (Figure 6). Perhaps the more opportunistic species were able to move further from the wave-disturbed end of the depth gradient because of the general degradation of community structure (i.e., the decline in species, individuals, biomass, and predator populations in the offshore). Only one of the community dominants from the 1970s showed this zonation shift, the haustoriid amphipods (Figure 5). The cluster analysis and the non-metric multidimensional scaling ordination also showed a broadening of depths zones, as the overlap in assemblages was greater in the 1990s (Figures 2 and 3). In addition, during the winter of 1997, deeper stations clustered closest to the next shallowest depth: 18 m near 9m and 9m near 6m (Figure 2), another indication of less distinct zonation. Another possible example of the shift in zonation was the decreased difference in species density between the 18 and 24 m depths by the 1990s (Table 3, Figure 4).

All the comments thus far concern the more frequently sampled south transect (Figure 1). However, the same

dramatic degradation of benthic communities at the end of the warm regime was also observed along the northern transect (Table 4). So, the decadal shift in benthic communities was present at all water depths along the two transects, which were over a kilometer apart and exposed to different levels of wave disturbance (Oliver et al. 1980).

Decadal shifts in marine ecosystems, similar to those in the Northeast Pacific, have been observed in relation to the Central Pacific Oscillation (Polovina et al. 1995, Venrick et al. 1987, Venrick 1997) and the North Atlantic Oscillation (Aebischer et al. 1990, Cushing 1995, Hurrell 1995, Pearce and Frid 1999, Weijerman et al. 2005). These were also primarily driven by climate changes resulting in mixing of deep-water nutrients into the photic zone. The main ecosystem response was bottom-up as increases in plankton production cascaded to higher levels in marine food webs, especially fisheries but also marine birds and mammals. In Antarctica, planktonic production is strongly influenced by changes in sea ice cover and light, but decadal regime shifts are still linked to oceanic climate variations with significant bottom-up responses in marine food webs (Ainley et al. 2005, but see Dayton 1989). Here, as in other latitudes, it can be difficult to separate decadal regime shifts from longer-term trends, for example a more continuous regional or global warming.

Alternate Hypotheses

Compared to El Viejo, El Niño events cause relatively short-term perturbations of the physical environment and therefore more short-term ecological responses, but there are longer-term impacts as well (Dayton and Tegner 1984, Tegner and Dayton 1987, 1991, Dayton et al. 1999). Large storms often accompany El Niño and the resulting wave disturbance has major impacts on marine bottom communities (Dayton and Tegner 1984). El Niño events even drive pulses of increased food to the deep-sea (Drazen et al. 1998), and these are linked to population fluctuations among the megafauna (Ruhl and Smith 2004). Nevertheless, there is no evidence that the decadal changes presented here are related to El Niño.

There was a significant El Niño in 1997-98, which did not result in abnormally large storm waves in Monterey Bay, but led to the highest regional annual rainfall on record (Wolter and Timlin 1998). Most of the rain fell between our third and forth sampling dates, so potential community impacts from deposition of fine sediment along the beach would have been detected only on the last sampling date (May 1998). However, community samples taken in May 1998 clustered closely with samples taken in July and September 1997 (Figure 2). The least similar samples were those collected during the winter (December 1997), well before most of the rainfall from the 1997-98 El Niño (Figure 2). This is the same seasonal pattern in community structure observed in the 1970s (Oliver et al. 1980). The winter depression in community structure was coincident with the season of maximum wave disturbance along the beach. Wave disturbance decreased throughout the spring, summer, and fall until the first winter storms arrived, usually in late October or November. Community structure was generally most similar from the late spring until the first winter storms (Oliver et al. 1980, Figure 2). So, the general seasonal pattern was the same in the 1970s and during the 1997-98 El Niño, and there was no evidence that deposition of fine sediment from record breaking El Niño runoff modified the beach community based on the first set of samples

collected after the rainy period (May 1998). The distribution of sediment grain size along the beach was also similar between the 1970s and 1990s (Table 4). Moreover, deposition of fine sediment from river runoff is expected in deeper water than our study area. The depositional sink on the continental shelf is centered in 80m in Monterey Bay (Griggs and Hein 1980, Eittreim et al. 2002). Shallower than 30-40m, wave-generated bottom currents seasonally resuspend fine particles, selecting for sandy grain sizes that grade from fine to coarse with decreasing water depth (Clifton et al. 1971, Hodgson and Nybakken 1973, Oliver et al. 1980, Eittreim et al. 2002). Therefore, finer sediment deposited in less than 30-40 m at the end of the 1998 winter would be resuspended and transported into deeper water by the next winter storms.

The most significant potential disturbance from El Niño is not from river input of fine sediment, but from large storm waves like those produced in the 1982-83 event (Dayton and Tegner 1984). However, ecological impacts from storm waves are likely to be less important along a high-energy sandy beach than along rocky shores, where attached organisms can be removed, including large plants that provide essential habitat for many other species (Dayton and Tegner 1984, Dayton et al. 1999). Animals living in shifting sands are well adapted to periodic scour and burial (Oliver et al. 1980). For example, even the large tube-dwelling onuphid polychaete, *Nothria*, which dominated the infaunal biomass in the 1970s, can burrow upwards through 30 cm of sediments dumped on them in several minutes in field experiments (Oliver and Slattery 1976). In addition, benthic animals along the subtidal beach can move offshore with increased wave disturbance and migrate shoreward in calmer conditions (Oliver et al. 1980, Morin et al. 1985). Community recovery from large storms moving sand along the beach is likely to take as much as a year or two, not many years or a decade (Oliver et al. 1977). These sandy substrates are routinely moved by waves (Clifton et al. 1971).

Changes in bottom water temperature in these subtidal habitats (6-24m) vary between $10-15^0$ C (Pennington and Chavez 2000), well within the tolerance range of temperate invertebrates (Ricketts and Calvin 1985, Clark 1993). Temperature per se is not likely to produce the dramatic community changes we observed along the Monterey Bay sand flats, but rather something that covaries with temperature like wave disturbance or plankton production (Clark 1993). In the rocky intertidal habitat, in contrast, air as well as surface water temperatures can have significant impacts on community structure (Barry et al. 1995, Sagarin et al. 1999).

The most competitive alternate explanation for the decadal changes we document is that we are observing an even longer-term warming trend in the California Current (Barry et al. 1995, Sagarin et al. 1999). At Hopkins Marine Station, just 25 km south of our study site, the abundances of southern species increased and northern species decreased between 1931-33 and 1993-94 in a rocky intertidal habitat (Barry et al. 1995, Sagarin et al. 1999). In addition to a long-term warming trend, which their observations support, the rocky intertidal pattern may be related to El Viejo. The intertidal fauna was first sampled in 1931-33 just after the end a cold regime. Although the end of this earlier cold regime is generally recognized as 1924 (Mantua et al. 1997), there are geographical variations in the timing of regime shifts (Schwing et al. 1998). At Hopkins Marine Station, the cold period probably ended later in 1929 (Breaker 2007). So the first sampling started three years after

over two decades of cold water in the California Current. By 1993-94, almost 20 years into a warm regime, the change in abundance of southern and northern ranging species was documented. As the authors point out, better resolution of this apparent ecological response to long-term warming will depend on future sampling. In the sandy bottom, we did not observe the arrival of any new southern species by the end of the warm period (1997-98), or the abundance shifts of species with northern and southern ranges that were documented by Barry et al. (1995) and Sagarin et al. (1999).

Our results are similar to the ecological shifts observed in oceanic ecosystems (Francis et al. 1998) and the deep-sea benthos (Wigham et al. 2003, Ruhl and Smith 2004, Bailey et al. 2006), where climate changes appear to impact ecosystems by causing significant variations in the quantity and quality of food, usually in a bottom-up process. If a longer-term climate trend impacts the sandy bottoms more than, or in addition to, El Viejo, we predict it will still be related to lower plankton productivity caused by warmer water preventing effective delivery of deeper nutrients to the photic zone (Roemmich and McGowan 1995, McGowan et al. 1998). A longer-term trend can be separated from the effects of El Viejo by sampling through the present cold regime. If a longer-term warming trend dominates, we should not see recovery of the rich benthic communities observed at the end of the last cold period (1971-75). If recovery occurs, it may take significantly longer than the degradation of community structure caused by the low production in a warm regime. It may take longer to degrade a community by depriving it of food than to develop one by providing food. This hypothesis can be tested by more frequent sampling early in the warm and cold regimes. Long-term patterns of ecosystem change cannot be understood without time-series sampling like those exemplified in the California Current of plankton (McGowan 1990, Roemmich and McGowan 1995, McGowan et al. 1998) and kelp forests (Dayton et al. 1999).

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