SPATIAL AND TEMPORAL PATTERNS OF ZOOPLANKTON BIOMASS IN MONTEREY BAY, CALIFORNIA, DURING THE 1991–1993 EL NIÑO, AND AN ASSESSMENT OF THE SAMPLING DESIGN

CHERYL L. BADUINI[1]
Moss Landing Marine Laboratories
P.O. Box 450
Moss Landing, California 95039

ABSTRACT

To estimate spatial and temporal zooplankton biomass, and the appropriateness of the sampling design, eighteen surveys were conducted in Monterey Bay, California, between November 1991 and August 1993. Vertical tows were taken to estimate zooplankton biomass in six regions of the bay on each survey day. In year 1, when 100-m vertical tows were made, zooplankton biomass peaked in January, March, and August; in year 2, when 50-m vertical tows were made, biomass peaked in April, August, and October. Mean zooplankton biomass differed significantly among seasons for both years, but trends differed between years. In year 1, mean biomass measured in the Davidson and oceanic seasons was significantly greater than in the upwelling season. In year 2, mean biomass measured in the upwelling and oceanic seasons was significantly greater than in the Davidson period. The seasonal trends in zooplankton biomass during this study were representative of similar trends for the phytoplankton cycle in Monterey Bay, which had a spring and an autumn bloom and decreased biomass in winter. Low zooplankton levels recorded in Monterey Bay during February and April 1992 and January and March 1993 were probably related to an El Niño–Southern Oscillation warm-water event (ENSO) in 1991–93. The sampling regime adequately revealed large-scale spatial (tens of km) and temporal (seasonal) differences in zooplankton biomass, but probably does not adequately describe smaller spatial and shorter temporal processes.

INTRODUCTION

Zooplankton occupy an important ecological role in the transfer of energy from primary producers to higher trophic levels of the Monterey Bay ecosystem (Baltz and Morejohn 1977; Chu 1982). They are primary prey for numerous vertebrates in Monterey Bay (Scheonherr 1989; Baduini 1995). Nevertheless, there is little understanding of the distribution, abundance, and seasonal cycles of zooplankton in the bay. In contrast, there is extensive information about the seasonal cycles of phytoplankton abundance in the bay (Bolin and Abbott 1963; Garrison 1976; Silver and Davoll 1976; Waidelich 1976; Schrader 1981). Silver and Davoll (1976, 1977) and Waidelich (1976) conducted net tows for zooplankton during their phytoplankton surveys, but recorded only displacement volume (ml/1,000 m^3) and collected few zooplankton samples. It is difficult to determine seasonality or spatial differences in zooplankton abundance with the few samples collected for these reports; it is also difficult to design a sampling scheme that adequately detects the appropriate scale of spatial and temporal patterns. For these reasons, I sampled zooplankton to estimate seasonal variation of biomass in Monterey Bay from November 1991 to August 1993. An additional objective of the study was to assess the ability of the sampling design to detect spatial and temporal patterns in zooplankton biomass.

Monterey Bay spans approximately 44.3 km and is exposed to the open ocean and the California Current system (figure 1). Its most prominent bathymetric feature is the submarine canyon that begins approximately 100 m offshore of Moss Landing Harbor and reaches a depth of 1,830 m. Hydrographic seasons include an upwelling season from March to August, an oceanic period from September through October, and the Davidson Current period from November to February (Skogsberg 1936; Bolin and Abbott 1963; Abbott and Albee 1967; Smethie 1973).

Coastal upwelling is driven by persistent northwest winds that characterize spring and early summer. The length of the upwelling season varies annually, and upwelling events may be sporadic at the end of the season. Upwelling also may occur after any period of persistent northwest winds; for example, Smethie (1973) documented an unseasonal upwelling event during the Davidson period in December 1971. With the relaxation of upwelling, the oceanic period is characterized by onshore flow of offshore waters. Oceanic periods are not always well marked (Bolin and Abbott 1963) and may be obscured by sporadic upwelling after the end of the upwelling season. During the Davidson Current period, the California Countercurrent surfaces between the coast and the California Current system and flows north. This results in onshore water flow, downwelling, and deep mixing along the coast (Smethie 1973).

Phytoplankton cycles generally follow a pattern

[1]Present address: Department of Ecology and Evolutionary Biology, UC Irvine, Irvine, CA 92697, cbaduini@uci.edu.
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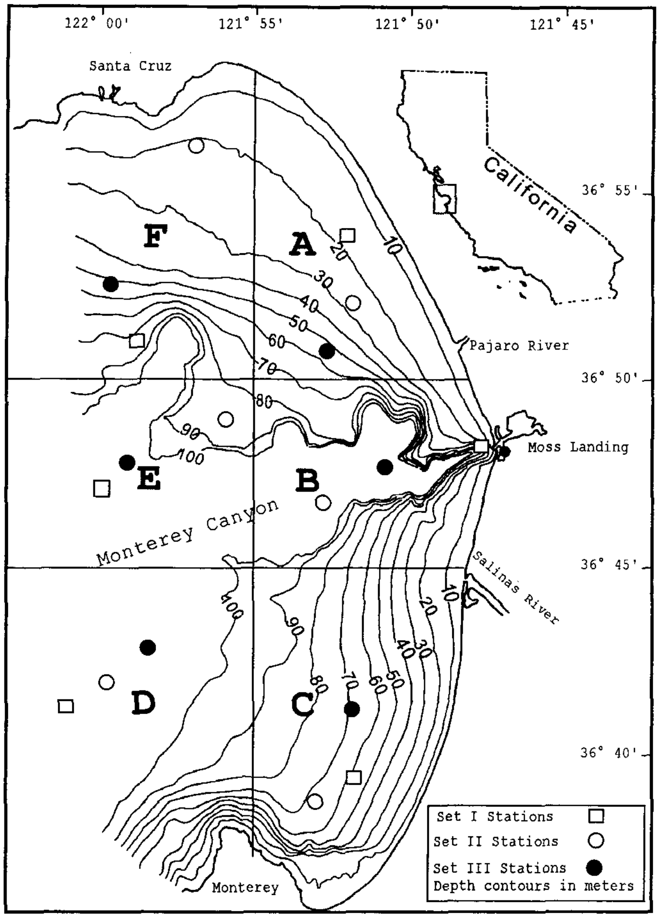

Figure 1. The six regions of the Monterey Bay study area: A, nearshore north; B, nearshore central; C, nearshore south; D, offshore south; E, offshore central; and F, offshore north.

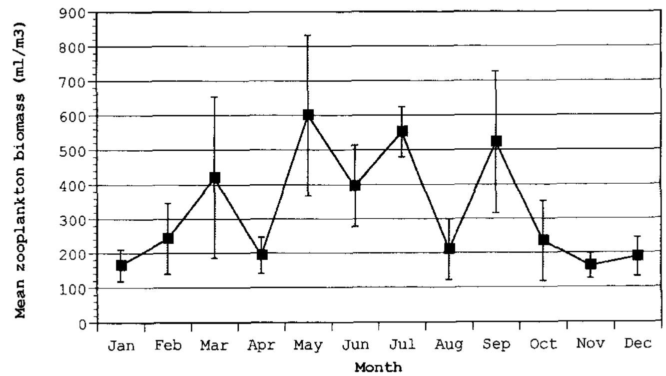

Figure 2. Seasonal cycle of zooplankton biomass (displacement volume) from data collected in Monterey Bay, Oct. 1971–Aug. 1972 (Waidelich 1976) and July 1975–July 1977 (two stations, #4 and #5; Silver and Davoll 1976, 1977). Error bars represent standard error.

similar to the hydrographic seasons, with low winter abundance due to low light levels and a well-mixed water column, a spring bloom associated with increasing light and enhanced nutrient concentrations, and an autumn bloom resulting from reduced zooplankton grazing (Waidelich 1976).

Zooplankton also follows a pattern similar to the hydrographic seasons, but is less well marked (figure 2; Silver and Davoll 1976, 1977; Waidelich 1976). In 1972, Waidelich (1976) observed a zooplankton maximum one month before the maximum of the phytoplankton spring bloom. This observation differs from those in other mid-latitude marine ecosystems, where the zooplankton bloom lags the phytoplankton bloom by about one month. Waidelich (1976) attributed this discrepancy to sampling error.

This paper reports the spatial and temporal patterns of zooplankton biomass in Monterey Bay, California. Samples were collected during the El Niño–Southern Oscillation event of 1991–93. This period was characterized by surface temperatures 1°–4°C greater than the mean from 1987 to 1992 in the same region (Sakuma et al. 1994a, b).

METHODS

Sampling Design

Eighteen zooplankton surveys were conducted in Monterey Bay from November 11, 1991, to August 17, 1993, with a vertically towed 335-μm, 0.5-m-diameter, 3-m-long, Puget Sound opening/closing plankton net (Research Nets). A precalibrated flowmeter (General Oceanics Model #2030) was mounted inside the mouth of the net to estimate water volume filtered per tow, except on five occasions when length of wire deployed and wire angle were used to calculate the volume filtered. Six regions of Monterey Bay were sampled on each cruise: A, nearshore north bay; B, nearshore central bay; C, nearshore south bay; D, offshore south bay; E, offshore central bay; and F, offshore north bay (figure 1).

One station was sampled per region (six stations total) on each survey day. Three sets of stations were chosen randomly and sampled throughout the study period: Sets I, II, and III (table 1). The offshore central station in Set I was chosen because it had been sampled historically (Bolin and Abbott 1963). To study temporal variability in zooplankton biomass, six fixed stations were sampled on every other survey throughout the study period (Set I stations). Six alternate stations were sampled one to two times per season in 1991–92 (Set II stations) and one to two times per season in 1992–93 (Set III stations). The additional sets (II and III) were added to increase the area sampled to determine spatial variability in zooplankton biomass. Because each survey event sampled a different water column at the same station than the previous survey, each sample was treated as a random sample (Cassie 1968).

Vertical zooplankton tows were collected as representative samples of seasonal zooplankton biomass in the

TABLE 1
Dates and Station Sets Sampled (X) for Zooplankton Surveys in Monterey Bay, November 1991 to August 1993

	Station set sampled		
Survey date	A	B	C
11/11/91	X		
11/21/91		X	
2/4/92	X		
2/18/92		X	
4/10/92	X		
4/28/92		X	
5/28/92		X	
7/23/92	X		
10/12/92	X		
11/5/92			X
12/16/92	X		
1/11/93			X
3/3/93	X		
4/19/93			X
8/4/93	X		
8/12/93		X	
8/17/93			X

upper water column. In 1991–92 (year 1), two replicate vertical tows per station were conducted from 100 m to the surface. In 1992–93 (year 2), two replicate vertical tows were conducted from 50 m to the surface. Because of differences in the sampling regime between years, each year was analyzed separately.

Samples were preserved in 10% buffered formalin in seawater (Salonen and Sarvala 1985). Large coelenterates were removed. Subsamples were taken with a Stempel pipette, filtered, rinsed with deionized water, and dried in an oven (Blue M) at 60°C ± 10° (Omori and Ikeda 1984) for at least 48 hrs. Aliquots were weighed with an electronic balance to the nearest 0.001 g. Total weight of the sample was then determined, and biomass was standardized to mg/m^3 on the basis of volume of water filtered.

Year 1 (November 1991 through September 1992) and year 2 (October 1992 through August 1993), consisting of 100-m and 50-m vertical tows, respectively, were analyzed individually because of a significant difference in biomass with depth. Each year was analyzed to determine the significance of differences in mean zooplankton biomass among seasons, regions, and sites (Underwood 1981; Zar 1984; SYSTAT 1992). Biomass estimates were logarithmically transformed to normalize data. Three oceanographic seasons were differentiated: upwelling (March to August), oceanic (September to November), and Davidson (December to February; Skogsberg 1936; Bolin and Abbott 1963; Abbott and Albee 1967; and Smethie 1973). Regions were north, central, and south, and sites were nearshore and offshore areas of the bay (figure 1). Tukey multiple comparison tests were used to determine the differences among significantly different seasons (Day and Quinn 1989).

Assessment of Sampling Design

Two pilot projects were conducted to assess the power of the sampling design. Ten replicate zooplankton tows were collected at one central nearshore station on March 31, 1992, to determine optimal replicate size. Precision (measured as standard error/mean) versus sample size was plotted along with cost per unit sample. Cost was measured as time required to complete an additional tow. Optimal replicate size was determined by calculating where the product of cost and standard error/mean was least.

Similarly, ten random samples were collected in the central nearshore region on March 31, 1992, to assess regional variability in zooplankton biomass and to determine an optimal number of tows per region. Precision and cost versus sample size were graphed to determine the optimal number of stations per region. The variability among stations in the central nearshore region was calculated to determine minimum detectable effect size of the regional replicate size used during this study.

RESULTS

Patterns of Zooplankton Biomass

The three random surveys per season (table 1) revealed that in year 1 (100-m vertical tows) zooplankton biomass peaked in January, March, and August; in year 2 (50-m tows) biomass peaked in April, August, and October (figures 3, 4).

Mean zooplankton biomass differed significantly among seasons for both years (year 1, $F = 4.26$, $n = 53$, $p = 0.020$; year 2, Kruskal-Wallis statistic = 6.02, $n = 96$, $p = 0.049$), but the trends differed between years (figure 5). In year 1 (100-m tows), mean biomass measured during the Davidson and oceanic seasons was significantly greater than during the upwelling season

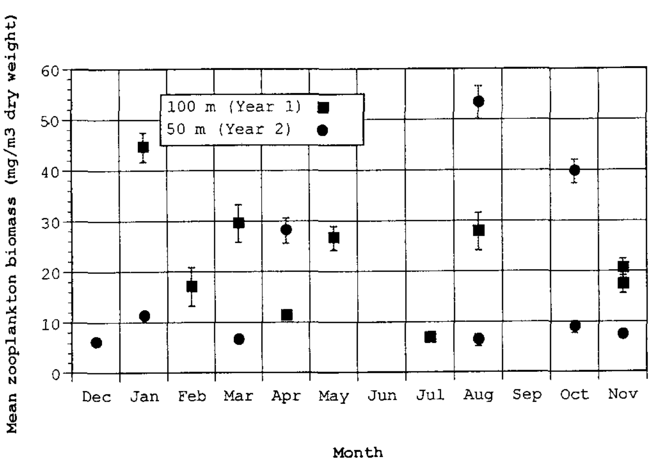

Figure 3. Mean zooplankton biomass estimates (mg/m^3 dry weight) per sampling date from November 1991 to August 1993 in Monterey Bay, California. Each point denotes mean biomass for all tows collected on each survey. Error bars represent standard error.

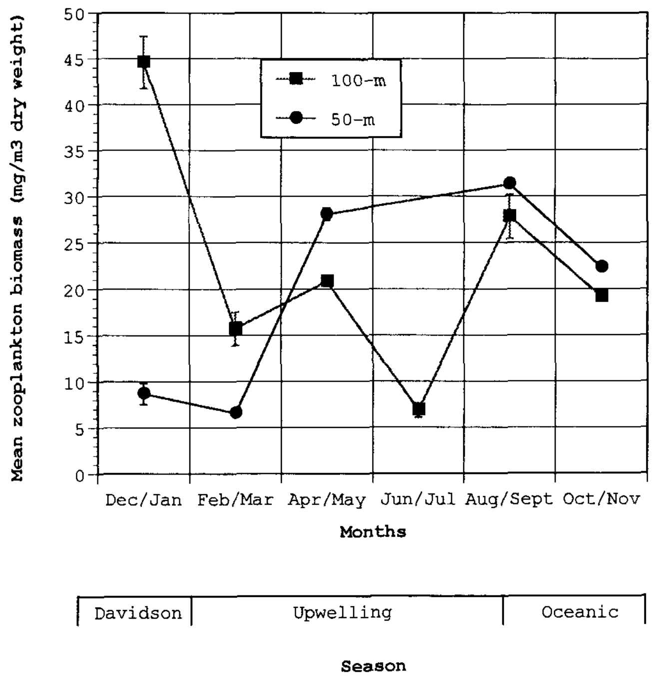

Figure 4. Mean bimonthly zooplankton biomass estimates (mg/m³ dry weight) from November 1991 to August 1993 in Monterey Bay, California. Error bars represent standard error.

(Tukey statistic = −0.24, n = 53, p = 0.015 for Davidson; Tukey statistic = −0.26, n = 53, p = 0.020 for oceanic; figures 4, 5). In year 2 (50-m tows), mean biomass measured during the upwelling and oceanic seasons was significantly greater than during the Davidson period (Tukey statistic = 0.25, n = 96, p = 0.040 for upwelling, and Tukey statistic = 0.29, n = 96, p = 0.032 for oceanic; figures 4, 5a).

There were no significant differences among regions of the bay within each year (figure 5b). Also, there were no significant differences between nearshore and offshore regions of the bay within each year, but the trend in biomass differs between years (figure 5c). In year 1, biomass was greater nearshore than offshore; in year 2, however, biomass was greater offshore.

Sampling Design

Precision (SE/mean) increased and stabilized after five replicate tows were sampled at a central nearshore station in Monterey Bay (figure 6a). Cost (time/unit tow) increased linearly with increasing number of samples. Optimal replicate size (where product of cost and precision was least) was three replicates per station. Only two replicates were conducted per station in this study.

Precision fluctuated and decreased as sampling effort increased within regional stations (figure 6b). Cost increased linearly with increasing sample size per region. Optimal sample size per region was two stations per region.

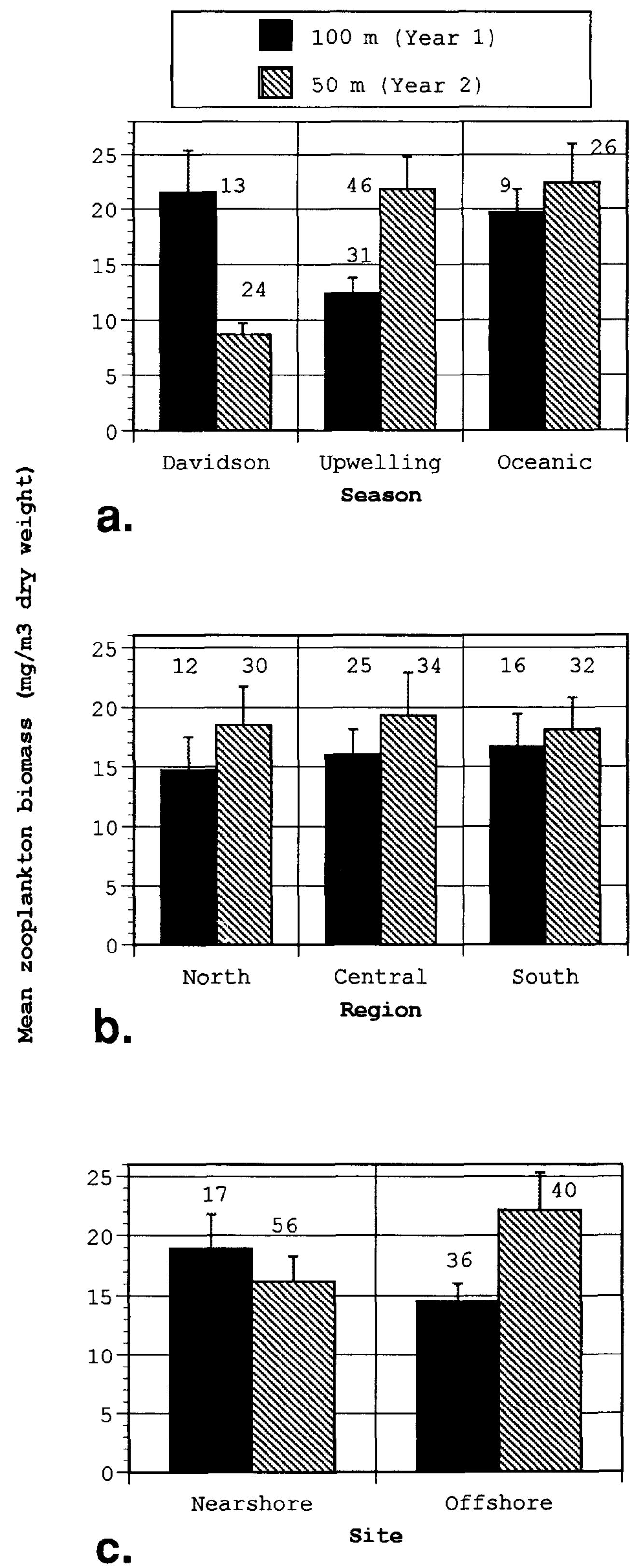

Figure 5. Mean zooplankton biomass estimates (mg/m³ dry weight) for 100-m (year 1) and 50-m (year 2) vertical tows: (*a*) by season; (*b*) by region; and (*c*) in nearshore and offshore areas of Monterey Bay, California. Error bars represent standard error. Sample sizes are indicated above bars.

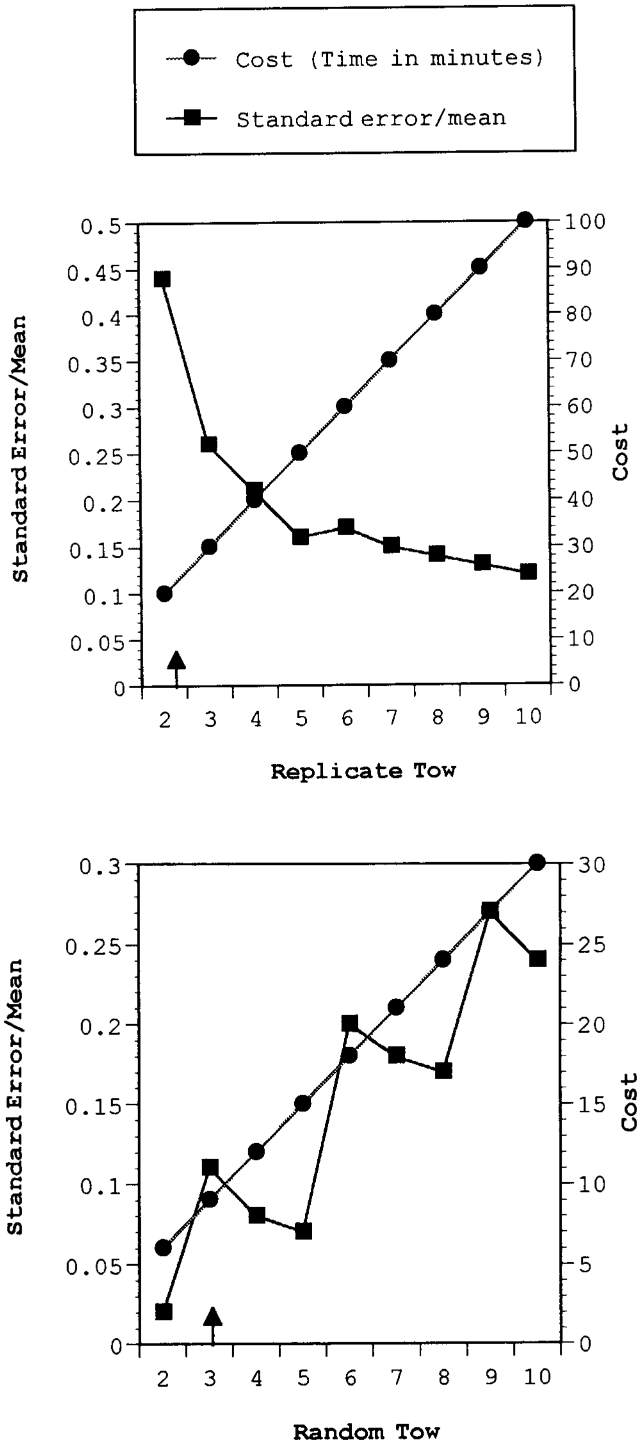

Figure 6. Estimates of precision (SE/mean) for zooplankton tows in Monterey Bay: *top,* ten replicate tows at one central nearshore station; *bottom,* ten random tows within the central nearshore region. *Arrows* indicate actual number of tows made during the study.

Assuming that the variability of the central nearshore region was representative of all six regions of this study, 3.3 samples per region were required to detect a doubling in zooplankton biomass. Three samples per region effectively detected a 2.6 increase in biomass.

DISCUSSION

Spatial and Temporal Distribution of Zooplankton Biomass

The seasonal trends in zooplankton biomass observed during both years of this study were representative of similar trends observed for the phytoplankton cycle in Monterey Bay, with a spring and autumn bloom and decreased zooplankton abundance in winter. A surprising result, however, was the high biomass collected in January of year 1 (figure 4). This may have resulted from a local upwelling event that may have occurred in the bay during that time.

Additionally interesting are the different seasonal trends observed between years. The different trends may have resulted because zooplankton were collected at different depths in the two years, and because this difference was statistically significant. Although the 100-m and 50-m tows were not collected in the same year, we will assume for comparison that trends would be similar between years for each tow depth. The greater biomass during the upwelling and oceanic seasons of year 2 may have resulted from upwelling events that brought greater biomass into surface waters, where it was detected in the relatively shallow, 50-m tows. This trend was not observed in year 1, possibly because biomass was calculated over a greater depth range (100 m) and thus the greater productivity in surface waters went undetected. However, two peaks in biomass occurred during the upwelling season of year 1, in May and August.

The low zooplankton levels recorded in Monterey Bay during February and April 1992 and January and March 1993 (figure 3) were probably related to an El Niño–Southern Oscillation warm-water event (ENSO) in 1991–93. Water temperatures were 1°–4°C higher near the surface in May–June 1992 compared with the mean for May–June 1987–92 (Sakuma et al. 1994a). Salinities were, on average, 0.8 ppt lower near the surface. Movement of California Current water inshore was the most likely explanation for the hydrography in 1992. Conditions during February to March 1993 off central California were characterized as a continuation of the ENSO that developed in early 1992 (Sakuma et al. 1994b). Temperatures throughout the water column (to 500 m) were cooler than for a similar period in 1992 (Sakuma et al. 1994b), but remained substantially warmer than the region's long-term average in the CalCOFI database. Surface temperatures were 1° to 3°C higher than the mean for 1983–93. The distribution of surface salinities and temperatures in May–June 1993 indicated an onshore displacement of California Current water similar to that seen in 1992 (Sakuma et al. 1994b). Additionally, female *Calanus* were less abundant in southern California waters in February and April 1992 than in 1989–91 (Mullin 1994).

Although there were low levels of zooplankton in the bay during several months in 1992–93, there was a large increase in zooplankton biomass from February to March and April to May 1992. There was a similar increase in biomass from March to April 1993 (figure 3). This may have been the period when the dampening El Niño effects were overcome by a pulsed upwelling event in the bay.

Sampling Design

Eighteen stations represented the spatial distribution of zooplankton biomass over the 550-km^2 area of Monterey Bay. This limited sampling scheme, however, revealed large-scale spatial differences in zooplankton biomass (the greater nearshore mean zooplankton biomass measured in 1991–92). The low precision determined for the central nearshore region also indicates that spatial resolution was limited. The precision curve never stabilized when ten random zooplankton tows were conducted over a 74-km^2 area.

Two to three surveys per season were conducted to determine temporal differences in zooplankton biomass. This sampling regime revealed large-scale temporal differences in zooplankton biomass (the seasonal differences within years), but probably does not adequately describe shorter temporal processes that may occur over days or weeks.

Although this study quantified the seasonal and spatial abundance of zooplankton biomass in Monterey Bay, there is little information about the seasonal diversity of zooplankton taxa in the bay. Calanoid copepods, particularly *Calanus pacificus*, dominated zooplankton samples collected at the surface in February and December 1991. Other taxa, such as zoea crab larvae, were abundant in autumn. It is unknown how the cycling of particular zooplankton communities affects the distribution and abundance of their vertebrate predators. Thus the effects of predation on the distribution and abundance of zooplankton taxa in Monterey Bay are incomplete and require further examination.

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